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A REVISION OF THE ARTEMISIA VULGARIS COMPLEX IN NORTH AMERICA†

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The north american allies of *Artemisia vulgaris* L, an Old World species, form a polyploid complex of great diversity, extending from Alaska to Guatemala, and from Hudson Bay and the Mississippi Valley to the Pacific. The center of this diversity lies in the western United States. The extent of the problem posed to the systematist by this group of plants is at once apparent by referring to the last two complete treatments of these species. Hall and Clements (1923) included under *Artemisia vulgaris* L., with fifteen subspecies, all the American forms which, but fifteen years previously, had been treated as fifty-four distinct species by Rydberg (1916).

These authors were alike in using comparative morphology as the principal tool in their taxonomic work, but their species concepts were at different poles from each other. Rydberg had come to believe that any striking morphological form deserved a name, and that this should be a specific name, since he could see no advantage in using trinomials. The significance of geographical range was rarely considered. Rydberg's species often represent morphologically well-marked forms, but all too frequently they are found to be thoroughly linked with others by intermediates, or to be unique variants, or to have no natural range of their own. Often his species are based on one morphological character, which is soon found to occur sporadically here and there

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over a large area in which other characters in the same plants show trends of variation in other directions. These limitations in Rydberg's species concept make his entities artificial rather than natural.

In their monumental monograph, Hall and Clements, at the other extreme, offered the most conservative species concept that could be defended on morphological grounds. The result was the telescoping of Rydberg's fifty-four species of this complex into one species, as mentioned above. Later evaluation of the same materials by other workers has shown that the fundamental units of Hall and Clements were carefully established. Other workers have upheld the majority of their basic units but have often treated their subspecies as species in order to conform with more widely accepted taxonomic practice. Hall and Clements' work is therefore sound from the morphological viewpoint, but the addition of one significant new criterion, chromosome number, has now made it possible to see a little more clearly the limits of the species in this group.

The present paper takes the consequences of this discovery and presents a study of many new collections that were not available to Hall and Clements. It also utilizes genetical, garden, and field studies as background data for the herbarium studies. Several members of this complex were grown in the varied environment experiments conducted by the Carnegie Institution of Washington along a transect across central California, and some cytological and genetical work was done on them. The results of these experimental studies have been reported by Clausen, Keck, and Hiesey (1940a). Additional forms have since become available for cytological study. The herbarium investigation was made at the time when the results from the transplant experiments were being prepared for publication, because the cytogenetic findings showed the need for a revised systematic treatment.

The investigations of Clausen, Keck, and Hiesey (1940a and b) showed that several ecospecies must be recognized in this polyploid complex. On the other hand, from a limited amount of evidence these authors suggested the possibility that, to use the biosystematic term, only one cenospecies was involved in the whole subsection *Vulgares* of *Artemisia*, i.e., that at least a limited amount of interbreeding and gene exchange could still take place among its members.

The morphological variation of the plants composing this complex is very great, making the delimitations of natural groups a difficult problem. The prominent characters of taxonomic use include size of parts such as leaves and heads, shape of leaves, and quality and quantity of the pubescence. Most of these are subject to environmental modification and must be interpreted with that in mind. Vegetative propagation by means of rhizomes is well developed in most of the species, and notable variations may be perpetuated for long periods in this manner. Under adverse climatic conditions, as in the far north and at alpine heights, it may be only the exceptional year in which these plants are able to propagate themselves sexually, although they are strongly

established in these localities (Hultén, 1937, p. 327; Clausen, Keck, and Hiesey, 1940a, p. 336). Furthermore, single characters, which some authors have utilized in the past to differentiate "species" in this group, have been found very undependable for this purpose. It is only when a group of characters is found correlated to each other within a given territory that the existence of a natural systematic unit can be surmised. Even then the systematist must reconcile himself to having a residue of specimens that he must arbitrarily include or exclude from a given unit of lower order, because natural crossings between such units produce recombinations that do not fit his key.

When historical precedent has entrenched a name in the botanical manuals, only a thorough revision of the group can properly appraise it. For example, Thomas Nuttall in 1818 proposed four species in this group. One, based on a specimen from near St. Louis, with leaves lightly tomentose on the upper surface and densely tomentose beneath, he named *A. ludoviciana*. A second, based on specimens from the Wisconsin area, with leaves white-tomentose on both sides, he named *A. gnaphalodes*. These two species have been maintained in the majority of botanical works down to the present, yet this writer agrees with Asa Gray that there is no warrant for separating these variations even in a subspecific category. The only characters that have been proposed for distinguishing them prove to be completely scattered in distribution, with every indication of complete interbreeding between the forms.

This revision employs orthodox taxonomy rather than experimental taxonomy (biosystematics), because the experimental evidence has been very incomplete. Consequently, it has not been possible to determine the exact genetic-ecologic boundaries of the various units, and thus to apply more than superficially the concept of species set down by Clausen, Keck, and Hiesey (1939a). Consequently, most reliance has necessarily been placed upon comparative morphology coupled with distribution; and all of the available cytological information has been used. In order to recognize units as comparable as possible with those determined by experiment, the geographic-ecologic principle has been followed in developing this species concept. That is, an attempt has been made to find key morphological distinctions that mark groups limited by natural environmental barriers, whether these barriers be geographical or ecological. From the kind and amount of intergradation observed between the natural units thus set off, the systematic category of the units has been determined.

Under the biosystematic concept of species at least partial genetic barriers exist between species. A difference in chromosome number is a genetic barrier to free intercrossing, and so it in itself may be taken as evidence that distinct species are involved, provided that morphological differences have had time to follow the genetic break. In the present group of species the differences in chromosome number coincide with major morphological breaks in each instance examined.

In the *vulgaris* complex the morphological breaks between species are only moderately distinct. This prompted Hall and Clements to keep all its units in one species. As compared with almost all the other species of the section *Abrotanum* to which this group belongs, the specific differences in the subsection *Vulgares* are not morphologically large. A gauge for species is set, however, by the chromosome data where they are known. With these as a basis, the other species have been delimited as regional groups of comparable order, showing relatively little intergradation.

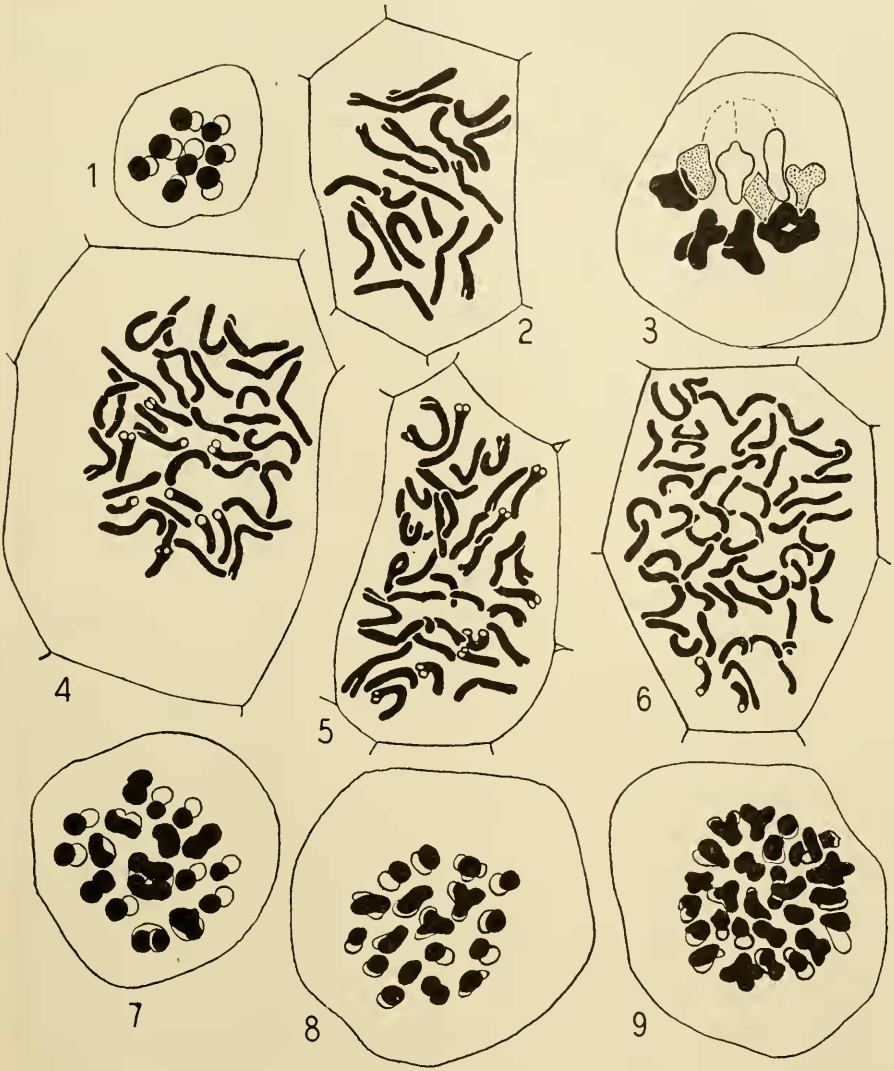
Regional groups that differ from each other in morphology and distribution, but that intergrade completely where their ranges overlap, appear to lack genetic barriers. Such units are treated as subspecies, and all of these are geographical. Because of the extensive morphological variation in these plants, requiring broad subspecies, it is likely that the larger subspecies contain more than one ecotype.

Morphological variants that from herbarium evidence do not appear to have either geographic-ecologic correlation or genetic barriers separating them are not named. These often striking variants are the *formae* of many taxonomists; but such uncorrelated forms cannot be considered of phylogenetic significance.

Cytological and Genetical Evidence. The chromosome numbers of 37 plants from eight American systematic units, including seven species, have thus far been determined in addition to the European *A. vulgaris.* These chromosome numbers have been reported previously by Clausen, Keck, and Hiesey (1939b, 1940a and b), but several additional collections are reported in this paper for the first time. The enumeration of the collections that have been counted follows the citation of specimens of the unit concerned.

The European *A. vulgaris* is a diploid species, with $n = 8$ chromosomes. In contrast, all the American forms of the *Vulgares* that have thus far been investigated follow a 9 series of chromosome numbers. This cytological difference alone is sufficient to keep all the American forms out of the Old World *vulgaris. Artemisia Carruthii* and *A. Suksdorfii* are diploid, with $n = 9$; *A. serrata, A. longifolia,* and *A. ludoviciana* sspp. *typica* and *incompta* are tetraploid, with $n = 18$; and *A. Douglasiana* and *A. Tilesii* ssp. *unalaschcensis* are hexaploid, with $n = 27$. Chromosomes of these forms are illustrated in figures 1–9. The two American diploid species thus far known, *A. Carruthii* and *A. Suksdorfii,* have larger chromosomes than any of the other forms including the diploid *A. vulgaris,* with the chromosomes of *A. Suksdorfii* the largest of all.

The little breeding work that has been done with these plants has for the most part been reported (Clausen, Keck, and Hiesey, 1940a). This report covered selfings of *A. Douglasiana* from Santa Barbara, and of *A. ludoviciana typica* from Manitou, Colorado, and also two pentaploid hybrids that were obtained when these two races were crossed. An additional cross has been attempted between *A. ludoviciana typica* from Leevining, California, and *A. Suksdorfii* from Trinidad, California, in the hope that *A. Douglasiana*



Figures 1–9. Heterotypic metaphases of meiosis in pollen mother cells and somatic metaphases in roots. Fig. 1. *Artemisia vulgaris*, Skåne, Sweden, 8_{II}. Fig. 2. *A. Carruthii*, Springer, New Mexico, $2n = 18$. Fig. 3. *A. Suksdorfii*, White Horse, Washington, 9_{II}. Fig. 4. *A. serrata*, St. Paul, Minnesota, $2n = 36$. Fig. 5. *A. longifolia*, Billings County, North Dakota, $2n = 36$. Fig. 6. *A. Douglasiana*, Medford, Oregon, $2n = 56$. Fig. 7. *A. ludoviciana typica*, Manitou, Colorado, $16_{II} + 1_{IV}$. Fig. 8. *A. ludoviciana incompta*, Yosemite Creek, California, 18_{II}. Fig. 9. *A. Tilesii unalaschcensis*, Unalaska, Aleutian Islands, 27_{II}. Enlargement for all figures: *ca.* × 2400.

might be synthesized through amphidiploidy, but it did not have a fair chance, because the races tested differed too much in time of flowering. The supposed amphidiploid origin of *A. Douglasiana* is discussed in more detail on page 459.

The Subsection in Perspective. The members of the *vulgaris* complex are widely distributed across the North American continent. There are two diploid species of radically different appearance. Along the Pacific shores of the United States from the Canadian boundary to northern California grows *Artemisia Suksdorfii,* a stout, large-leaved herb in clumps often more than a meter high and half again as broad. On the more arid plains and plateaus from western Kansas and Colorado to Chihuahua is *A. Carruthii,* a low gray clump with tiny fascicled leaves, in marked contrast with the preceding diploid.

Through the midlands of the continent there is a group of tetraploids perplexing in their variation. On the periphery it is relatively simple to disjoin *A. serrata* and *A. longifolia* from the mass, the former in the upper Mississippi Valley, and the latter spreading somewhat westward from the prairies and badlands of the Dakotas. The remainder goes through an impressive amount of variation across the western half of the United States and down the length of Mexico, sometimes in accord with the climatic zone occupied, and again in seeming contradiction to the environment. From the lowlands and plains this distribution may be traced up through the timbered slopes to the alpine summits, and from the regions of abundant rainfall out across the arid desert ranges. No lines of demarcation of even relative sharpness are at first apparent, for even the regional facies of the assemblage show rather frequent intergradation. As a consequence, this tetraploid diversity is gathered under one specific name, *A. ludoviciana.* The regional races of individual caste within it are demarked as subspecies—seven in all. Where the sampling has been dense, as in Colorado, the abundance of examples makes the broad gamut of variation appear but the more confusing; however, from this it becomes apparent that the number of specific barriers to interbreeding in this assemblage is strictly limited—that the variation is intra-, rather than inter-specific. In Mexico, on the other hand, additional sampling may well uncover regional subspecies too poorly discerned for recognition at present. The potential variation is certainly there. The increased sampling available to us now has resulted in the recognition of the validity of *sulcata* and *albula* as subspecies of *ludoviciana* from the arid Southwest, while the same abundance of material has failed to develop any substantial basis for separating *gnaphalodes* from *ludoviciana,* or *Wrightii* from *Carruthii,* all of these results running at variance with rather recent conclusions drawn from less material.

The two known hexaploids are *A. Douglasiana,* from a Pacific Coast region between *A. Suksdorfii* and *A. ludoviciana,* respectively its diploid and tetraploid presumed progenitors, its individuals becoming the largest in all the complex; and *A. Tilesii,* a coarse herb with two subspecies distributed from the Pacific Northwest to the Arctic Ocean and to the western shore of Hudson Bay, but obviously coming to our continent from Asia, for the trail is clear

both across Bering Strait and the Aleutians to Kamchatka, and westward to European Arctic Russia. Its near-relatives remained in the Old World.

The chromosome numbers of *A. Michauxiana* and *A. Lindleyana* are not known as yet, and that information is desirable for the completion of the picture. The alpine *A. Michauxiana* is a quite well-marked entity with its small, much dissected and finely cut leaves, its large heads and low stature, and its near-restriction to the northern Rockies. *Artemisia Lindleyana* is a suffrutescent plant—a distinction from the usual herbaceous forms—with a distinctive subracemose inflorescence but somewhat variable leaves. Its distribution is a natural one along the low elevation watercourses of the Columbia River system.

The least well-known member of the complex is *A. Prescottiana*, an anomalous species of airy aspect due to its long filiform divided leaves, sparse raceme, and very slender branching stem. The root is gone from the only specimen I have studied, but it might even have been annual. David Douglas collected it six score years ago on the Quick Sand River, near The Dalles, but it seems to have escaped recollection, and it appears to be uncertain today even as to along which stream Douglas found it.

Other conclusions on the derivations of the various systematic units that can be gathered from the several lines of evidence available are presented in the discussion following the systematic treatment (pp. 465–467).

Methods, Materials, and Acknowledgments

From the early stages of the investigation it was apparent that a study of this complex in any one herbarium would be very inadequate because of the great variability found in nature and the broad geographic distribution, and that it would be essential to bring together an abundance of herbarium material for comparison. Consequently, the material from twelve herbaria was assembled for simultaneous comparison at our central laboratory at Stanford. In the case of the more widely distributed collections, this made possible the comparison of all the material from one locality at one time. On account of the variation within one habitat, this is a much safer method than comparing the materials in one herbarium at a time.

So many herbarium specimens have been studied that their citation in entirety becomes impractical. Distribution maps therefore indicate wherever possible the approximate location of each collection, leaving for the citation lists only a limited number of collections. These have been chosen because they are reasonably representative and widely distributed to herbaria, or because they mark the range or otherwise have special interest. Citation is more complete for those groups that are rare, or that were previously understood inadequately. The complete documentation is to be found in those herbaria in which material was studied and annotated. In so far as possible citation is by counties in a north to south and east to west geographical sequence; the county name is followed by a colon.

The descriptions are cross-comparable and made as brief as permissible if they are to have a utilitarian value in a group marked by so great diversity. The distribution and ecological data are gathered from the herbarium specimens and from some personal field knowledge of the group.

During the taxonomic investigation collections were studied and annotated in the following herbaria. The abbreviations are those employed in the citation of specimens. In those herbaria marked with an asterisk, only selected groups were examined:

C—University of California, Berkeley.
CAS—California Academy of Sciences, San Francisco.
CI—Carnegie Institution of Washington, Stanford University, Calif.
*Minn—University of Minnesota, Minneapolis.
NY—New York Botanical Garden, New York.
Ph—Academy of Natural Sciences of Philadelphia.
Po—Pomona College, Claremont, Calif.
RM—Rocky Mountain Herbarium, University of Wyoming, Laramie.
SU—Dudley Herbarium, Stanford University, Calif.
US—United States National Herbarium, Smithsonian Institution, Washington, D. C.
*UW—University of Washington, Seattle.
Veg—Vegetation Type Map Herbarium of U. S. Forest Service, University of California, Berkeley.

To the curators of these herbaria grateful acknowledgment is made for the privilege of study generously afforded and for other help given. I am indebted to the late Sir Arthur W. Hill, Director of the Royal Botanic Gardens at Kew, for the loan of a few types and pertinent specimens from that institution. Particular thanks are due my colleague, Dr. Jens Clausen, for critical aid in making taxonomic and cytologic judgments. To him also, together with my colleague, Dr. W. M. Hiesey, I am grateful for a critical reading of the manuscript.

SYSTEMATIC TREATMENT

The great diversity of this group of plants has been mentioned. One of the most variable organs, which at the same time furnishes key characters of importance, is the leaf. In figure 10 some of this variation is shown in order to enable the reader to visualize the type of leaf-cut which words often inadequately describe. One is not to assume that this illustration encompasses by any means the entire range of variation that is to be encountered in these systematic units, but these drawings are intended to supplement the key.

KEY TO THE SYSTEMATIC UNITS

A. Divisions of lower leaves again lobed or cleft, 5–15 mm. wide, directed forward, green and essentially glabrous above. Old World; eastern North America ..... 1. *A. vulgaris*

AA. Divisions of lower leaves entire, or if lobed, the divisions less than 5 mm. wide, spreading, or leaves themselves entire.

B. At least some of the leaves bipinnately parted with salient segments again toothed. Northern Rocky Mts. ..... 2. *A. Michauxiana*

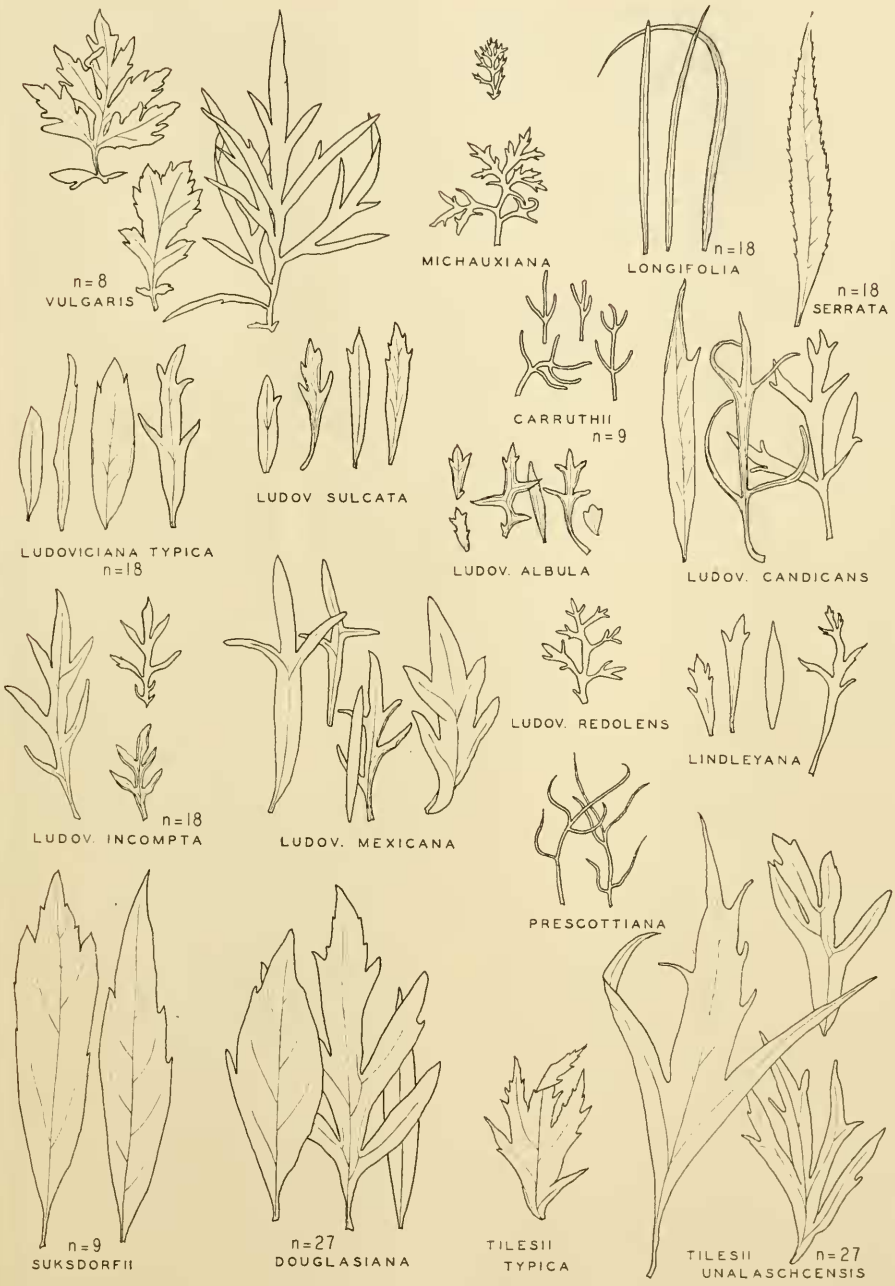


Figure 10. Typical leaf outlines in *Artemisia* subsection *Vulgares*. × 2/5.

BB. Leaves entire to bipinnatifid with entire lobes.
C. Leaves linear to linear-lanceolate, entire, or rarely divided into few usually caudate lobes, often caudate and revolute-margined, the tomentum on the upper surface usually deciduous, 3–12 cm. long; involucre 4–5 mm. high. North Dakota to central Wyoming ..... 3. *A. longifolia*
CC. Leaves not as above, or if slender and entire the involucre shorter.
D. Leaves finely and evenly serrate, strongly discolored; plant 1–2.5 m. tall; heads only 2 mm. wide. Upper Mississippi Valley ..... 4. *A. serrata*
DD. Leaves not finely and evenly serrate.
E. Leaves fascicled, 1–3 cm. long only, divided into divaricate linear-filiform lobes 0.5–1 mm. wide; panicle narrow, spike-like; herbage mostly gray-tomentose (leaves sometimes green on upper surface), the heads tomentulose and ± shining. Kansas and Arizona to northern Mexico ..... 5. *A. Carruthii*
EE. Leaves not fascicled, or if fascicled their divisions more more than 2 mm. wide or bright green.
F. Involucre as high as or higher than wide (except in *A. ludoviciana candicans*, but in that the leaves not prominently discolored).
G. Principal leaves narrow, 1 cm. or less wide exclusive of lobes when present, tomentose on both sides or green above; stems rarely more than 1 m. tall.
H. Herbaceous to base ..... 6. *A. ludoviciana*
I. Principal leaves entire or merely lobed.
J. Leaves 3–10 cm. long, the margin not revolute.
K. Panicle usually compact, elongated, not leafy; leaves not thin, usually white-tomentose on both sides, rarely bright green on upper surface; involucre 3–4 mm. high. Ontario and Mississippi Valley to Washington and California.
6a. *A. ludoviciana* ssp. *typica*
KK. Panicle open, leafy (sometimes contracted); leaves thin, usually bright green above, white-tomentose beneath; involucre 2.5–3 mm. high. Arizona to Chihuahua ..... 6b. *A. ludoviciana* ssp. *sulcata*
JJ. Leaves mostly 1–2 cm. long, lanceolate, thickish, usually white-tomentose on both sides, the margin often narrowly rev-

olute; panicle open, the heads pendant in slender ± leafy racemes. Southwestern U. S. and northern Mexico.

6c. *A. ludoviciana* ssp. *albula*

II. Principal leaves ± parted or divided.

L. Involucre 4–5 mm. high, 4–7 mm. wide; leaves white-tomentose on both sides, plane. Western Montana to northern Utah and California. . 6d. *A. ludoviciana* ssp. *candicans*

LL. Involucre 2.5–3.5 mm. high, 2–3.5 mm. wide; leaves usually green on upper surface (sometimes tomentose on both sides in *incompta*).

M. Panicle spike-like or racemose; disk-florets 15–45. Montane; Montana to Utah and California.

6e. *A. ludoviciana* ssp. *incompta*

MM. Panicle broader, branching, leafy; disk-florets 6–18.

N. Lower leaves 5–10 cm. long, pinnately or ternately divided, the lobes entire, strongly discolored. Southwestern U. S. to southern Mexico.

6f. *A. ludoviciana* ssp. *mexicana*

NN. Lower leaves 2–5 cm. long, bipinnately dissected, green and ± glandular, or moderately tomentose on under surface. S.W. Texas to S.E. Arizona and Durango.

6g. *A. ludoviciana* ssp. *redolens*

HH. Suffrutescent with woody base; leaves narrow, entire to serrate-dentate apically, rarely more deeply lobed; panicle narrow, spike-like or racemose. Banks of Columbia River and tributaries. . . . . 7. *A. Lindleyana*

GG. Principal leaves broader, 1–5 cm. wide exclusive of lobes when present, frequently entire, lobes if present few, short, entire, discolored; stems frequently more than 1 m. tall.

O. Involucre terete or narrow-ovoid, less than 2 mm. wide, yellow-green and shining; ray-florets 3–7; disk-florets 2–8; leaves green above, silvery tomentose beneath. Immediate Pacific Coast and Puget Sound region.....8. *A. Suksdorfii*

OO. Involucre campanulate, 2–3 mm. wide, ± tomentose; ray-florets 6–10; disk-florets 10–25; leaves less strikingly discolored. Western Washington to northern Baja California.....9. *A. Douglasiana*

FF. Involucre wider than high.

P. Stem branching at base; herbage very sparingly arachnoid-pilose, somewhat more densely so (but not tomentose) on under surface of leaves; leaves pinnatifid with 3–7 filiform divisions less than 1 mm. wide; inflorescence racemose. Columbia River.....10. *A. Prescottiana*

PP. Stem unbranched at base; leaves tomentose on under surface, strongly discolored, deeply incised, the divisions wider; inflorescence a spike-like panicle.....11. *A. Tilesii*

Q. Inflorescence overtopped by the leaves; involucre 4–5 mm. high, 6–9 mm. wide; heads 30–125-flowered. Siberia to Hudson Bay.....11a. *A. Tilesii* ssp. *typica*

QQ. Inflorescence well exceeding the leaves; involucre 3–5 mm. high, 4–8 mm. wide; heads 30–55-flowered. Northern Japan, Kamchatka, Alaska to Pacific Northwest. 11b. *A. Tilesii* ssp. *unalaschcensis*

1. **Artemisia vulgaris** L., Sp. Pl. 848, 1753.

Figures 1 and 10

Type statement: "Habitat in Europae cultis, ruderatis."

Stems 5 to 15 dm. tall, slender to moderately stout, herbaceous to base, commonly unbranched; lower leaves obovate to deltoid-ovate in outline, deeply incised into 3–7 lance-ovate to narrowly lanceolate principal divisions, which are for the most part again irregularly and sharply toothed or lobed, the lobes and teeth all directed forward, 5–12 cm. long, often nearly as wide, green and glabrous or nearly so above, densely white-tomentose beneath, the margin obscurely revolute; inflorescence an ample leafy panicle with ascending branches crowded with subsessile heads, 3–15 cm. broad; heads medium-sized, erect or nodding; involucre campanulate, 3–4 mm. high, 2.5–3.5 mm. wide, moderately tomentose, with 9–13 bracts; ray-florets 6–9; disk-florets 13–20.

Common throughout Europe and eastward to Siberia; probably adventive in North America, but in places appearing indigenous, occurring irregularly from Newfoundland to Manitoba and Alabama.

Material of this species was examined in only three herbaria. In addition to the localities cited by Hall and Clements (1923), collections should be reported from the states of New Hampshire, Vermont, Massachusetts, and North Carolina.

The chromosomes were counted in meiosis of plants grown from seed collected in Skåne, southern Sweden, and kindly sent by Dr. Göte Turesson.

2. **Artemisia Michauxiana** Bess. in Hook., Fl. Bor. Amer. 1:324, 1833.

Figures 10 and 11

Type statement: "Rocky Mountains. *Douglas.* Columbia. *Douglas, in Herb. Lindl.*" The type is in the Lindley Herbarium, according to a note attached to a sheet in the Bentham Herbarium at Kew, which is said to correspond exactly with the type (*fide* R. A. Rolfe). This Kew sheet has been labeled in Douglas' hand, "In fissures of dry rocks near the Kettle Falls and sources of the Columbia. 1826." A piece of this sheet was removed and sent to New York, where it has been labeled as part of the type. The first collection cited doubtless came from the Rocky Mountains of Canada; the second may have come from the state of Washington.

Artemisia discolor Dougl. ex Bess., Bull. Soc. Nat. Mosc. 9:46, 1836. The type has been studied on loan from Kew. It was collected "on rocky situations near Spokane and the Kettle Falls," by David Douglas. It is a somewhat coarser plant than the type of *A. Michauxiana,* which came from a higher elevation, but the two can scarcely be separated morphologically. Its inflorescence is considerably more open-paniculate than that of *Michauxiana,* but this character proves to be variable and lacking in geographic significance in this region as is also the vesture of the herbage.

A. graveolens Rydb., Bull. Torr. Club 24:296, 1897. Leaves greener than in the type of *Michauxiana,* but much dissected and to be classed here rather than in *incompta.* Type locality: Yogo Baldy, Little Belt Mts., Montana.

A. subglabra A. Nels., Bull. Torr. Club 27:36, Jan. 24, 1900. The same form as *A. graveolens.* Type locality: stony banks of Yellowstone River, near Yancey's, Yellowstone Park, "no. 5743."

A. tenuis Rydb., Mem. N. Y. Bot. Gard. 1:431, Feb. 15, 1900. A slender, small-headed form of *graveolens,* i.e., the green form of the species. Type locality: Emigrant Gulch. Park Co., Montana.

A. vulgaris ssp. *discolor* Hall et Clem., Carn. Inst. Wash. Publ. 326:74, 1923.

A. vulgaris var. *discolor* Jeps., Man. Fl. Pl. Calif. 1141, 1925.

A. vulgaris ssp. *Michauxiana* St. John, Res. Stud. St. Coll. Wash. 1:106, 1929.

A. vulgaris ssp. *Michauxiana* var. *typica* St. John, *ibid.*

A. discolor var. *glandulifera* Hend., Rhodora 32:27, 1930. Leaves not tomentose beneath but glandular. Type locality: eastern base of Steins Mts., Harney Co., Oregon.

A. vulgaris var. *glandulifera* Peck, Man. Higher Pls. Ore. 766, 1941.

Stems 2–4(–7) dm. tall; herbage white-tomentose throughout when young to nearly glabrous and green; leaves short and broad, rather crowded, commonly bipinnately divided with the secondary segments again toothed, the linear lobes widely spreading, acute, rarely elongated, even the uppermost leaves rarely entire, 2–5 cm. long, typically bright green above and white-

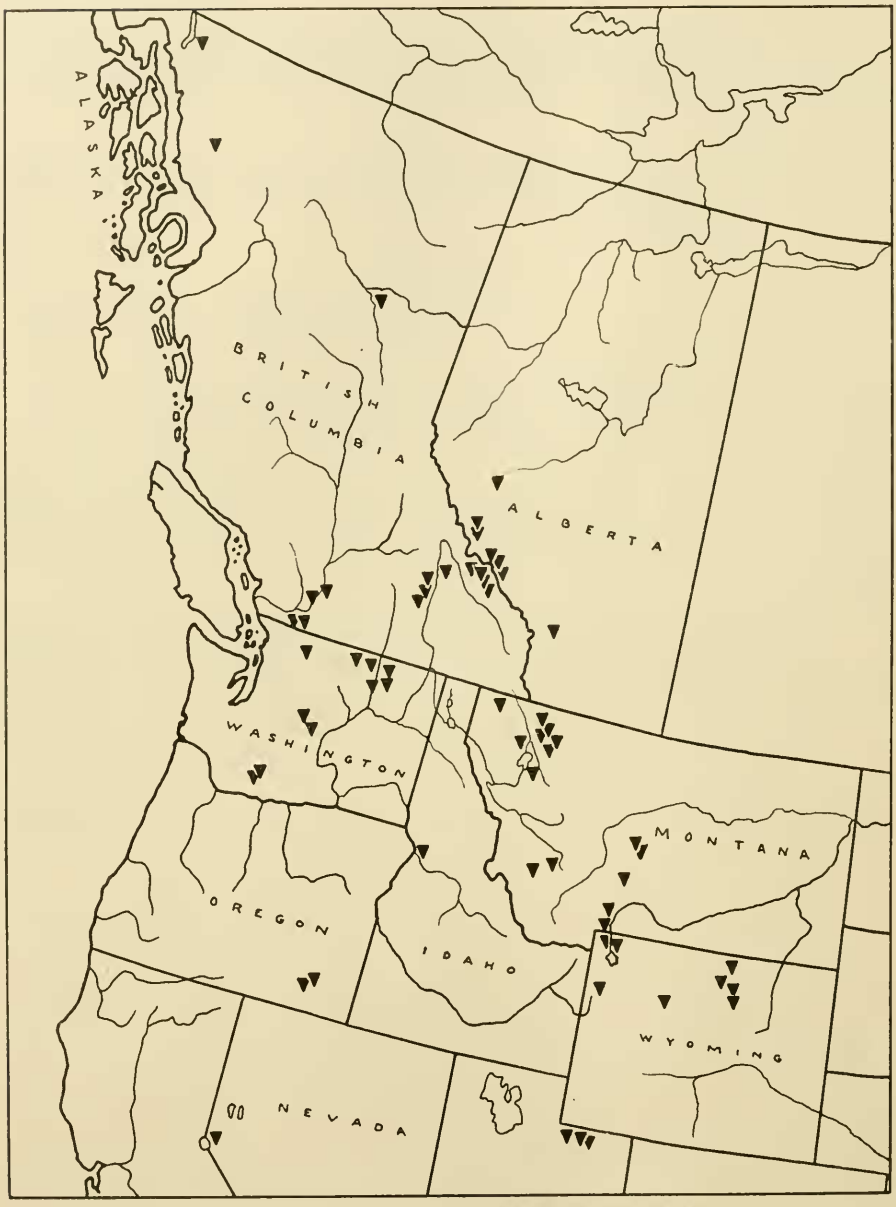


Figure 11. Distribution of *Artemisia Michauxiana*.

tomentose beneath, the margin plane or narrowly revolute; inflorescence a slender racemose or spike-like panicle, occasionally more open, not leafy; heads large, nodding at least at first; involucre hemispheric, 3.5–4 mm. high, (2.5–)3.5–5 mm. wide, glabrous or sparingly tomentose, with 9–16 bracts; ray-florets 9–12; disk-florets 15–35.

Rocky Mountains of northern Alberta and British Columbia, southward through the mountains to northern Wyoming, northern Idaho, and central Washington; local in Steins Mountains, Oregon, and in Washoe County, Nevada. Occurring at elevations of 500 to 2750 meters, and flowering from July to August.

Alberta. Moberly's on Athabaska, *Schaffer 1612;* Cataract Creek, *Brown 1471;* Poboctan Pass; Lake Louise; Vermilion Mt.; Highwood River District, *Brinkman 3209.* British Columbia. Mt. Atlin, Lake Atlin region, *Swarth 177;* Telegraph Creek, *Walker 1208.* Cariboo: Mt. Selwyn, *Raup and Abbe 3946.* Kootenay: Mt. Whaleback, Yoho Park, *Ulke 334;* Mt. Wapta; Kicking Horse River; Carbonate Draw, Selkirk Mts., *Shaw 335;* Goldstream; Revelstoke. Yale: Fraser Valley; Lake House, Skagit River, *Macoun 76927.* New Westminster: Yale; Chilliwack Valley. Montana. Glacier: Midvale, *Umbach 275;* Many Glacier. Flathead: Avalanche Lake; Columbia Falls, *Williams 709;* Mission Creek. Lincoln: Tobacco Mts. Judith Basin: Yogo Baldy, Aug. 24, 1896, 7000 ft., *J. H. Flodman 881* (NY, type of *A. graveolens*); Long Baldy, Little Belt Mts., Aug. 19, 1896, 7–8000 ft., *Flodman 881* (US, labeled isotype of *A. graveolens*). Deer Lodge: Ryans Lake; Mt. Haggin. Gallatin: Mt. Bridger. Park: Emigrant Gulch, 6500 ft., *Rydberg and Bessey 5201* (NY, type of *A. tenuis;* isotype, US); Electric Peak. Wyoming. Sheridan: Little Tongue River Canyon, *Williams 3233.* Johnson: headwaters of Clear Creek and Crazy Woman River (NY). Big Horn: Doyle Creek, *Goodding 385.* Park: Meeteetse Creek, *Griffiths.* Yellowstone Park: Yellowstone River near Junction Butte, *Nelson 5743* (RM, type of *A. subglabra;* isotype, NY). Teton: Leigh Lake, *Williams 994.* Utah. Summit: Blacks Fork, Uinta Mts.; Upper Henry's Fork Basin, *Maguire et al. 14412, 14586.* Idaho. Idaho: mouth of Salmon River, *Eastwood 13337.* Washington. Okanogan: Oroville; Mt. Chapaca, *Elmer 589;* Tonasket; Hidden Lakes; Angels Pass, *Thompson 7033.* Whatcom: Newhalem, *Muenscher 9919.* Chelan: Nigger Creek; Three Brothers. Yakima: Mt. Adams, *Suksdorf* (C). Oregon. Harney: Steins Mts., *Cusick 1991;* alpine rivulet near eastern base of Steins Mts., beyond Alvord, *Henderson 8489* (CAS, isotype of *A. discolor* var. *glandulifera*). Nevada. Washoe: head of Galena Creek, 8500 ft., *Heller 10222.*

The exact southern limits of this species are difficult to determine on morphological criteria alone. Plants from the alpine zone in parts of Nevada, as in the Ruby, White, and Charleston mountains, which appear very similar to the *tenuis* form of *Michauxiana,* are referred in this paper to *A. ludoviciana* ssp. *incompta.* This is because intergrades seem to connect these forms with very narrow, dark green leaf-segments with forms having the more usual type of *incompta* leaf, and these *Michauxiana*-like forms are fairly well isolated from the other members of *Michauxiana.* Their disposition would be more satisfactorily made if cytological data were available.

3. **Artemisia longifolia** Nutt., Gen. 2:142, 1818.

Figures 5, 10, and 12

Type statement: "In rocky situations, on the banks of the Missouri, from the confluence of White River to the Mountains?" A single leaf preserved at the Philadelphia Academy, labeled "Artemisia longifolia Missouri" in Nuttall's hand, is doubtless from the type.

A. ludoviciana var. *integrifolia* A. NELS., First Rep. Fl. Wyo. 138, 1896. Based upon *A. integrifolia* of Pursh, Fl. Amer. Sept. 2:520, 1814. Not *A. integrifolia* L., 1853. Pursh attempted to identify a specimen collected on bluffs of the Missouri River, October 1, 1804, by Lewis, no. 53, with the Linnaean species. Lewis' specimen at the Philadelphia Academy has been examined.

A. natronensis A. NELS., Bull. Torr. Club 26:485, 1899. A wide-leaved form of the species. "Type no. is 568, Willow Creek [Wyoming], July 20, 1894, distributed as a variety of A. ludoviciana."

A. falcata RYDB., N. Amer. Fl. 34:271, 1916. The form with salient linear lobes on the very narrow leaves, but in all other respects typical. Found on the southeastern border of the range of this species; the type locality is Fort Pierre, South Dakota.

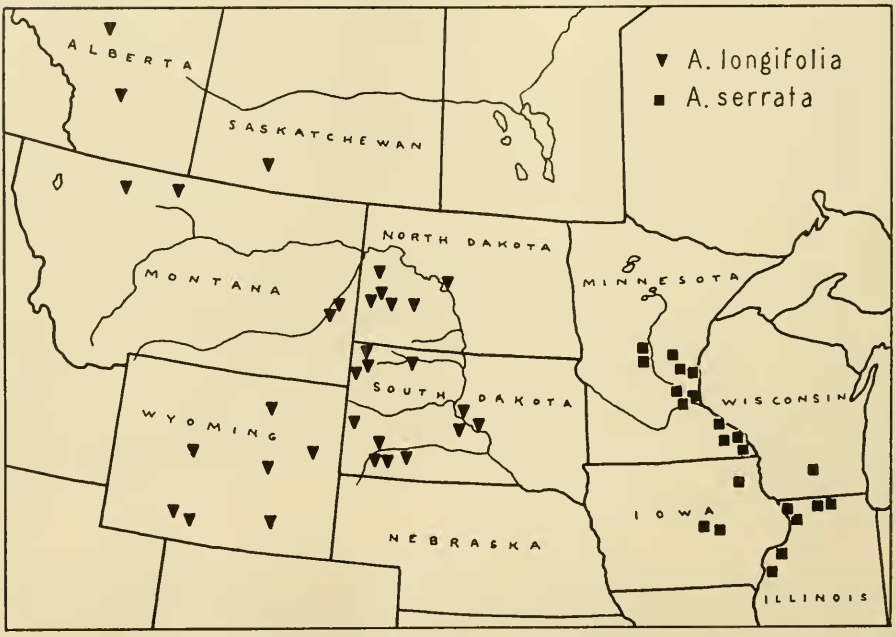


Figure 12. Distribution of *Artemisia longifolia* and *A. serrata*.

A. vulgaris ssp. *longifolia* HALL et CLEM., Carn. Inst. Wash. Publ. 326:78, 1923.
A. vulgaris var. *longifolia* PECK, Man. Higher Pl. Ore. 767, 1941.

Stems 2–8 dm. tall, usually rather stout, erect, herbaceous down to the woody caudex, white-tomentose; leaves linear or linear-lanceolate, merely acuminate or, more often, caudate-attenuate, usually entire, sometimes with a few slender teeth or lobes, occasionally the lobes caudate-elongated, 3–12 cm. long, 2–5 (–6) mm. wide, those of the inflorescence very narrow and short, all loosely floccose and usually becoming glabrate or green above, densely tomentose beneath, often strongly revolute; inflorescence a strict short paniele, sometimes elongated or rather open; heads mostly erect and peduncled; involucre campanulate or ± turbinate, 4–5 mm. high, 3–4 mm. wide, tomentulose to densely tomentose, with 9–17 bracts; ray-florets 3–10; disk-florets 8–26. $n = 18$.

Prairies and badlands from Saskatchewan and Alberta to central North and South Dakota, eastern Montana, and southern Wyoming, often in heavy alkaline clays. Flowering from July to September.

Saskatchewan. 1858, *Bourgeau.* Alberta. W. of Lacombe, *Moss;* Rosedale, *Moodie 1097.* North Dakota. McLean, Morton, McKenzie, Stark, Billings, and Golden Valley counties. South Dakota. Evarts, Missouri River; Grand River. Stanley: Fort Pierre, Sept. 29, 1897, *Griffiths 757* (US, type of *A. falcata;* isotype, US; phototypes, C, NY, US). Washabaugh: Pine Ridge Reservation. Washington: Sheep Mt. Harding: Glaring Fork; Short Pine Hills. Lawrence (?): Crow Buttes. Pennington: Big Bad Lands, *Osterhout 7529.* Montana. Milk River. Dawson: Colgate, *Sandberg et al. 1011;* Glendive. Toole: Shelby, *Jones.* (Po). Wyoming. Natrona: Willow Creek, *Nelson 568* (RM, type of *A. natronensis;* isotype, Minn). Johnson: Lake DeSmet, *Nelson 8545.* Carbon: Como Ridge near Medicine Bow, *Osterhout 6290.* Converse: Badlands, T. 38, R. 68. Fremont: Muskrat Creek, *Goodding 517.* Sweetwater: Table Rock; Point of Rocks, *Nelson 8148.*

Chromosome counts were made in root-tips of four plants from Billings County, North Dakota. The living plants were supplied us through the kindness of Mr. E. C. Moran.

4. **Artemisia serrata** Nutt., Gen. 2:142, 1818.

Figures 4, 10, and 12

Type statement: "Near the Prairie du Chien, on the banks of the Mississippi, also on the banks of the Missouri, in open alluvial soils." Upper Louisiana, *Nuttall* (Ph, type).

Artemisia ludoviciana var. *serrata* Torr. et Gray, Fl. N. Amer. 2:420, 1843.
A. vulgaris ssp. *serrata* Hall et Clem., Carn. Inst. Wash. Publ. 326:79, 1923.

Stems 10–25 dm. tall, virgate, herbaceous; leaves lanceolate to linear-lanceolate, acuminate, sharply and rather finely serrate from apex well down toward base (rarely subentire), 8–12(–15) cm. long, 12–20 mm. wide, those of the inflorescence prominent but gradually reduced in size, all dark green and glabrous above, white-tomentose beneath; inflorescence a leafy panicle 5–15 cm. broad; heads small, mostly erect, rather crowded; involucre campanulate, 2.3–3 mm. high, *ca.* 2 mm. wide, slightly floccose, with 8–12 bracts; ray-florets 6–11; disk-florets 3–16. $n = 18$.

Upper Mississippi Valley; Minnesota to Illinois and Iowa; introduced in New York. Flowering from July to September.

Illinois. Winnebago, Jo Daviess, Rock Island, and Henderson counties. Wisconsin. Dane: *Wibbe* (US). Minnesota. Chisago: Taylors Falls, *B. C. Taylor.* Isanti: *Sandberg* (C). Mille Lacs: Milaca, *Sheldon 3278.* Stearns: Grand Lake; Rockville, *Campbell.* Hennepin: Fort Snelling; Minnesota River near mouth of Nine Mile Creek. Wabasha: Lake City. Winona: Wiscoy, *Holzinger;* Winona. Houston: Jefferson. Iowa. Fayette: *Fink 406.* Poweshiek: Grinnell. Jasper: Baxter (US).

Chromosome counts were made in root-tips of two plants from St. Paul, Minnesota. These plants were supplied through the kindness of Dr. C. O. Rosendahl.

5. **Artemisia Carruthii** Wood ex Carruth,

Trans. Kans. Acad. Sci. 5 : 51, 1877.

Figures 2, 10, and 13

Type locality: Kansas. Type not seen.

Artemisia Wrightii GRAY, Proc. Amer. Acad. 19:48, 1883. The type collection, *Wright 1279*, made at Santa Rita del Cobre, Grant Co., New Mexico, is scarcely morphologically distinguishable from material from the type region of *Carruthii*. The leaves are greener and glabrate on the upper surface in *Wrightii*, tomentose in *Carruthii*, but this feature does not appear in this case to distinguish ecotypes or geographical subspecies. While the *Wrightii* form does not occur to the eastward, it grows together with the typical form at many localities in New Mexico. The very broad range of overlapping of the two forms largely obscures any difference in ecological preference that may exist between them, although the incipient stages of ecotype formation may be involved.

A. kansana BRITT. in Britt. and Brown, Ill. Fl. 3:466, 1898. A form identical with *Carruthii*. Type locality: Lane County, Kansas.

A. coloradensis OSTERH., Bull. Torr. Club 27:506, 1900. Leaf-segments unusually wide, otherwise indistinguishable. In the type, from Dale Creek, Larimer Co., Colorado, the segments are less than 1 mm. wider than those of *Carruthii* from Kansas, but other collections from the same county are broader and intergrade toward the *Brittonii* form of *A. ludoviciana typica*.

A. Bakeri GREENE, Pl. Baker. 3:31, 1901. Allied to the *Wrightii* form in that the leaves are green on the upper surface, but these are atypically scattered and wide, giving some suggestion of an extremely narrow-leaved form of *A. ludoviciana mexicana*. This does not appear to warrant separation from the more usual forms of *Carruthii*, however, for plants of this appearance are found in the western portion of the range of the species in scattered stations between which more typical forms are found. In other words, the variant is of spasmodic occurrence and by no means of uniform appearance. The inflorescence is usually open-paniculate. Type locality: canyon of the Gunnison River, near Cimmaron, Colorado.

A. Pringlei GREENM., Proc. Amer. Acad. 40:50, 1904. Heads larger than usual, containing twice the average number of florets for the species as a whole in the type collection (*ca.* 18 involucral bracts, 14–18 ray-florets, 20–34 disk-florets), but subject to considerable variation in the region from which the type came. Not readily separable by any character from *Carruthii*. Type locality: plains near the city of Chihuahua.

A. Wrightii coloradensis A. NELS. in Coult. and Nels., Man. Rocky Mt. 568, 1909.

A. mexicana Bakeri A. NELS., *ibid.* 569.

A. vulgaris ssp. *Wrightii* HALL et CLEM., Carn. Inst. Wash. Publ. 326:80, 1923.

A. vulgaris var. *Wrightii* PALMER et STEYERM., Ann. Mo. Bot. Gard. 22:677, 1935; Rhodora 40:134, 1938.

A. vulgaris Carruthii F. C. GATES, Trans. Kansas Acad. Sci. 42:138, 1940.

A. Carruthii var. *Wrightii* BLAKE, Jour. Wash. Acad. Sci. 30:472, 1940.

Stems 3–6 dm. tall; herbage white-tomentose throughout or the upper surface of the leaves green; leaves divided into divaricate linear-filiform lobes, these sometimes again toothed, 1–3 cm. long, those of sterile shoots and of the inflorescence often entire, reduced, the margin closely revolute; inflorescence a leafy narrow spike-like panicle, 1–3 cm. wide, occasionally rather expanded;

Figure 13. Distribution of *A. Carruthii.*

heads small, nodding when young; involucre campanulate, 3–3.5 mm. high, 1.5–3 mm. wide, tomentulose, often shining, with 8–14 bracts; ray-florets 6–14; disk-florets 6–20. $n = 9$.

Western Kansas and northern Texas to central Utah, Arizona, and northern Chihuahua, at elevations from 800 to 3000 m. Adventive in Rhode Island, Indiana, Missouri, and eastern Kansas. Flowering from late July through September.

KANSAS. Rooks: Rockport. Lane: plains, Aug. 15, 1895, *Hitchcock 302* (NY, type of *A. kansana;* isotypes, RM, US). Greeley: Tribune. Kearney: *Hitchcock.* Hamilton: Syracuse, *Rose and Fitch 17010.* Clark: *White.* Meade: Meade. Seward: Liberal. TEXAS. Potter: Amarillo, *Bailey 128.* Randall: Paloduro Canyon. COLORADO. Larimer: Dale Creek, Sept. 7, 1899, *Osterhout 2010* (RM, type of *A. coloradensis;* isotypes, NY, Po, RM). Eagle: Red Cliff. Park: Como. Douglas: Pine Grove. El Paso: Palmer Lake; Colorado Springs. Teller: Florissant. Fremont: Canon City; Wet Mountain Valley. Saguache: Marshall Pass, 10,000 ft., *Baker 879;* San Luis Valley. Montrose: Bedrock. Gunnison: Black Canyon, *Baker 698* (C, NY, Po, RM, SU, US, topotypes of *A. Bakeri*). Ouray: 5 mi. N. of Ouray. San Miquel: Norwood Hill. Huerfano: Cucharas Valley. Costilla: La Veta Pass. Mineral: Wagon Wheel Gap. Hinsdale: Lake City. Archuleta: Piedra. La Plata: W. of Hesperus. NEW MEXICO. Union: Folsom. Colfax: Ute Park. Rio Arriba: Dulce. San Juan: Tunitcha Mts., *Standley 7622.* Quay: Nara Visa; Llano Estacado. San Miguel; Las Vegas. Santa Fe: Canoncito. Sandoval: Jemez Springs. Valencia: Grants. Lincoln: Ruidoso. Dona Ana: Organ Mts. Socorro: Negrito Ranger Station. Catron: Patterson. Grant: Santa Rita del Cobre, *Wright 1279* (Gray Herb., type of *A. Wrightii;* isotype, NY; phototypes, C, NY); N. of Cliff. Hidalgo: Cloverdale, *Mearns 456.* UTAH. Sevier: Mt. Marvin, *Rydberg and Carlton 7567.* Piute: Circle Valley. Garfield: Panguitch Lake. San Juan: Montezuma Canyon, E. of Monticello, *Rydberg and Garrett 9687;* Elk Mts.; Bluff. ARIZONA. Apache: Carrizo Mts., *Standley 7510;* Greer. Navajo: Oraibi, *Voth 76.* Coconino: Grand Canyon; Mt. Humphreys; 7 mi. E. of Flagstaff; Bellemont, *Jones 4074;* Williams. Mohave: Hualpai Mts., *Kearney and Peebles 12727.* Yavapai: Prescott. Gila: Black River Bridge. Greenlee: Metcalf. Graham: Mt. Graham. Cochise: Chiricahua Mine, *Blumer 1794.* CHIHUAHUA. Lake Santa Maria; plains near Chihuahua, *Pringle 625* (Gray Herb., type of *A. Pringlei;* isotypes, Ph, SU, US); Santa Eulalia Plains, *Wilkinson.* CHIHUAHUA or COAHUILA. Charco de Grado, Oct. 1852, *Thurber 791.* SONORA. San Luis Mts., *Mearns 2461;* Badehuachi, *Lloyd 404.*

Chromosome counts were made in root-tips of three plants grown from seed from Springer, Colfax County, New Mexico, and kindly supplied by Mrs. Gladys Nisbet.

In Colorado, on the one hand, occasional collections appear to be intermediate with the *Brittonii* form of *A. ludoviciana typica,* while in New Mexico, on the other, certain collections are found that are intermediate with *A. ludoviciana mexicana.* More chromosome counts will help clarify this situation and show whether, as is now suspected, all forms of *ludoviciana* are tetraploid, and of *Carruthii* diploid.

6. **Artemisia ludoviciana** Nutt., Gen. 2: 143, 1818.

6a. **Artemisia ludoviciana** Nutt. ssp. **typica** Keck, Carn. Inst. Wash. Publ. 520:330, 1940.

Figures 7, 10, and 14

Type statement: "On the banks of the Missisippi, near St. Louis; also on the alluvial plains of the Missouri." A specimen at Philadelphia from St. Louis, collected and starred by Nuttall, is the type. It consists of only four leaves, lightly tomentose above and densely tomentose beneath. Another Nuttall specimen at Philadelphia, labeled by Nuttall "Artemisia Ludoviciana. Platte plains," is not starred, but is a large branch in flower with all leaves entire and tomentose on both sides.

Artemisia ludoviciana NUTT., *loc. cit.*

A. gnaphalodes NUTT., *ibid.* Type statement: "On dry savannahs about Green Bay, Lake Michigan, and on the banks of Fox river, and the Missouri." A starred specimen at the Philadelphia Academy, collected by Nuttall at St. Louis, was considered by Hall and Clements to be the type, but its location is inconsistent with the type statement. It consists merely of the top of a flowering stem, in which the leaves are white-tomentose on both sides. See discussion of this synonym on p. 423.

A. Purshiana BESS. in Hook., Fl. Bor. Amer. 1:323, 1833. Type locality: "On the plains of the Saskatchewan. *Dr. Richardson. Drummond.*" See the following.

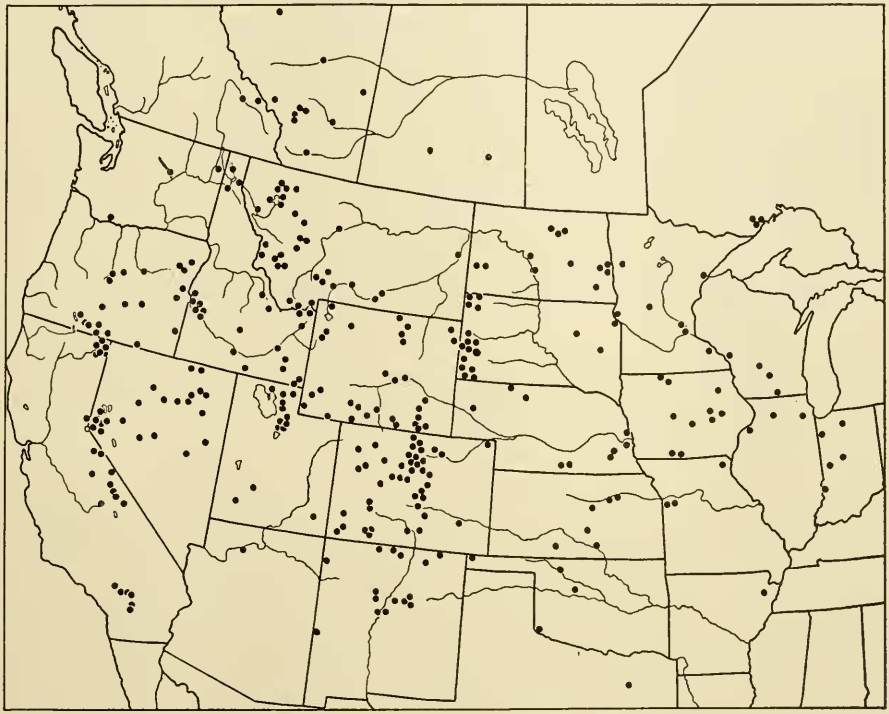


Figure 14. Distribution of *A. ludoviciana* ssp. *typica.*

A. Purshiana α *latifolia* BESS., *ibid.* Specimen at Kew (Herb. Hooker), which has been studied, taken in the Rocky Mts. by Drummond, is doubtless of the type collection. By his var. *latifolia,* Besser meant the typical form of *Purshiana* (as both species and variety seem to rest on the same type) as contrasted with his var. β *angustifolia,* also described here and based on a plant from "Red River. *Douglas, in Herb. Lindl.,*" which is said to have lanceolate leaves 1½ inches long and 3 lines wide. From this description it appears probable that this variety, too, is referable here.

A. ludoviciana var. *gnaphalodes* TORR. et GRAY, Fl. N. Amer. 2:420, 1843.

A. ludoviciana var. *latifolia* TORR. et GRAY, *ibid.*

A. vulgaris var. *gnaphalodes* O. KUNTZE, Rev. 1:309, 1891.

A. vulgaris var. *ludoviciana* O. KUNTZE, *ibid.*

A. rhizomata A. NELS., Bull. Torr. Club 27:34, 1900. A narrow-leaved form. Type locality: Sweetwater River, Wyoming.

A. rhizomata var. *pabularis* A. Nels., *ibid.* A small form of the preceding. Type locality: Red Desert, near Creston, Wyoming.

A. diversifolia Rydb., Bull. Torr. Club 28:20, 1901. A form with the principal leaves merely pinnately cleft, but the few lobes very narrow and acuminate. It closely resembles forms of ssp. *candicans* from the general region of northern Idaho, and should perhaps be interpreted as a transitional form. Type locality: Priest River, Idaho.

A. silvicola Osterh., Bull. Torr. Club 28:645, 1901. A form with lanceolate, nearly entire, strongly discolored leaves and large heads. Type locality: MacIntyre Creek, Larimer Co., Colorado.

A. Brittonii Rydb., Bull. Torr. Club 32:129, 1905. Leaves short, with 3 to 5 short rather divergent lobes, heavily tomentose on both sides. Type locality: Golden, Colorado.

A. pudica Rydb., *ibid.* 130. Inflorescence loosely branched, the large heads nodding, leaves rather thin and elongated. A spasmodic variant from widely scattered stations in the Colorado Rockies. Perhaps usually a shade modification. Type locality: Gunnison.

A. pabularis Rydb., *op. cit.* 33:157, 1906.

A. gnaphalodes diversifolia A. Nels. in Coult and Nels., Man. Rocky Mt. 569, 1909.

A. mexicana silvicola A. Nels., *ibid.*

A. Herriotii Rydb., Bull. Torr. Club 37:455, 1910. A large-leaved form from Edmonton, Alberta.

A. cuneata Rydb., N. Amer. Fl. 34:269, 1916. Leaves cuneate obovate, with a few salient teeth around the wide apex. Type locality: Idaho Springs, Colorado.

A. argophylla Rydb., *ibid.* 274. A robust form with exceptionally large heads. The type, from Longs Peak, Colorado, is well east of the range of ssp. *candicans,* which form it resembles.

A. vulgaris ssp. *ludoviciana* Hall et Clem., Carn. Inst. Wash. Publ. 326:76, 1923.

A. vulgaris ssp. *gnaphalodes* Hall et Clem., *ibid.* 77.

A. ludoviciana var. *pabularis* Fern., Rhodora 47:248, 1945.

A. ludoviciana var. *Brittonii* Fern., *ibid.*

A. ludoviciana var. *cuneata* Fern., *ibid.*

Stems 3–10 dm. tall, slender to moderately stout, herbaceous to base; leaves many, linear to lanceolate, oblanceolate or elliptic, sometimes cuneate, entire or few-toothed or -lobed especially apically, the lobes regularly entire, 3–10 cm. long, permanently and densely white-tomentose on both sides or loosely floccose to green and glabrate above, plane; inflorescence an elongated usually compact panicle, 1.5–5 cm. broad; heads medium-sized, erect or nodding, often in glomerules; involucre ovoid to campanulate, 3–4 mm. high, 2–3 mm. wide, usually densely tomentose, occasionally glabrate, with 7–13 bracts; ray-florets 5–12; disk-florets 6–21. $n = 18$.

Lowlands and mountains up to middle elevations (2200 m., or occasionally up to 2900 m. in the Colorado Rockies) from Ontario to Alberta, Washington, California, New Mexico, and Arkansas; sporadically introduced from Indiana to Virginia, New England, and Quebec. Flowering from July through September.

Ontario. Thunder Bay: near Fort William. Saskatchewan. Assiniboia, Indian Head, *Macoun 10984;* Ribstone Creek; Moose Jaw, *Johnson 969.* ? province, plains of the Saskatchewan, *Drummond* (Kew, type(?) of *A. Purshiana* var. *latifolia*). Alberta. Stettler District, Donalda to Bashaw; Peace River; Grand Prairie; Edmonton, *Macoun and Herriot 72825* (NY, type of *A. Herriotii*); Rosedale, *Moodie 1183;* Banff; Lethbridge. British Columbia. Kootenay: Beavermouth, *Shaw 1153;* Natural Bridge, *Ulke.* Indiana. Marshall, Fulton,

Newton, and Sullivan counties. Illinois. Dupage, Ogle, and Rock Island counties. Wisconsin. La Crosse, Sauk, Dane, and Rock counties. Minnesota. St. Louis, Norman, Traverse, Winona, Pope, and Hennepin counties. Iowa. Emmet, Fayette, Linn, Benton, Poweschiek, Boone, and Decatur counties. Missouri. Clark: *Mead*. Jackson: Sibley. Arkansas. Craighead: S. of Jonesboro, *Demaree 7179*. North Dakota. Cass, Ranson, Stutsman, Benson, Burleigh, McLean, and Golden Valley counties. South Dakota. Grant, Spink, Kingsbury, Harding, Butte, Meade, Lawrence, Custer, and Fall River counties. Nebraska. Douglas, Cass, Lancaster, Kearney, Brown, and Cherry counties. Kansas. Riley, Saline, McPherson, Sedgwick, and Pratt counties. Oklahoma. Woods, Cimmaron, Kingfisher, and Harmon counties. Texas. Wood: *Reverchon 3961*. Montana. Richland, Glacier, (Glacier National Park), Flathead, Sanders, Lewis and Clark, Yellowstone, Cascade, Carbon, Sweetgrass, Park, Gallatin, Jefferson, Deer Lodge, Silver Bow, Ravalli, and Beaverhead counties. Wyoming. Crook, Albany, Sheridan, Johnson, Natrona, Park (Yellowstone National Park), Teton, Lincoln, Carbon, Sweetwater, and Uinta counties. Colorado. Sedwick: Julesburg. Weld: New Windsor. Larimer: McIntyre Creek, Aug. 24, 1900, *Osterhout 2242* (NY, type of *A. silvicola;* isotypes, C, RM, US); Meadows Inn, Longs Peak, Aug. 14, 1907, *Clements* (NY, type of *A. argyrophylla*). Boulder: Foot of Flagstaff Mt., *Ewan in Pl. Exsic. Gray. 897*. Routt: S. of Steamboat Springs. Jefferson: Golden, Oct. 8, 1882, *N. L. Britton* (NY, type of *A. Brittonii*). Grande: Hot Sulphur Springs. Clear Creek: Idaho Springs, *Shear 4617* (NY, type of *A. cuneata*). Rio Blanco: Buford. Garfield: Glenwood Springs, *Eggleston 14982*. Otero: La Junta. Fremont: Canon City, *Brandegee 501*. Huerfano: Cucharas Valley. Alamosa: Alamosa. Gunnison: Gunnison, *Baker 573* (NY, type of *A. pudica;* isotypes, C, CAS, Po, RM, US). Mineral: Pagosa Peak, *Baker 634*. San Miquel: Norwood Hill. Montezuma: Mesa Verde National Park. New Mexico. Colfax: Raton. Rio Arriba: Brazos Canyon; Dulce. San Juan: Tunitcha Mts. San Miguel: Las Vegas. Sandoval: Sandia Mts., *Ellis 125*. Grant: mts. near Condes Camp, *Wright 1275*. Utah. Rich: Bear Lake, *Hammond 3879*. Box Elder: Corinne. Weber: Ogden Canyon. Salt Lake: Parleys Park. Piute: Marysvale, *Jones 5846*. San Juan: Dry Wash, Abajo Mts., *Ryberg and Garrett 9615*. Iron: Parowan. Arizona. Coconino: Grand Canyon, *Eggleston 15665*. Idaho. Bonner: Slough beach, forest between Priest Lake and East Fork, 630 m., *MacDougal 190* (NY, type of *A. diversifolia;* Clarks Fork Valley near Horse Plains, *Leiberg 1582*. Kootenai: Coeur d'Alene, *Leiberg 1552*. Lemhi: Gilmore. Fremont: Henry's Lake, *Nelson 6796*. Bannock: Lava. Bingham: Blackfoot. Blaine: Ketchum. Twin Falls: Shoshone Falls, *Nelson and Macbride 1366*. Gem: Sweet, *Macbride 1626*. Nevada. Elko, Eureka, Lander, Humboldt, White Pine, Nye, Pershing, Churchill, Washoe, Ormsby, Storey, and Lyon counties. Washington. Pend Oreille: Kalispell Lake. Chelan: Lake Chelan. Klickitat: Columbia River, *Suksdorf 1610*. Oregon. Wallowa, Union, Baker, Grant, Deschutes, Crook, Malheur, Harney, Lake, and Klamath counties. California. Modoc, Nevada, Mono, Inyo, San Bernardino, and Riverside counties.

Chromosome counts were made both in root-tips and in meiosis of one plant from Manitou and of two plants from Engelmann Canyon, all from El Paso County, Colorado, and in root-tips only of one plant from Leevining, Mono County, California, and of two plants from Upper Fern Valley, San Jacinto Mts., Riverside County, California.

An additional very interesting tetraploid, whose chromosomes were counted in root-tips, is now referred here. It was collected in Poopenaut Valley, Tuolumne River, Yosemite National Park, at 1065 m. elevation, *Nobs 1* (CI, RM). This plant, from the midst of the area occupied by the hexaploid *A. Douglasiana,* near the western base of the central Sierra Nevada, was presumed to be a peculiar form of that species when first studied. It had dis-

colored leaves like *Douglasiana*, but these were extremely narrow; those on the upper half of the stem were several centimeters long but less than 5 mm. wide. The lower leaves were oblanceolate and wider (up to 20 mm. including lobes), with rather short forward-projecting lobes in the outer half, precluding the possibility that this could be a form of *A. ludoviciana* ssp. *incompta* carried down from higher elevations. This plant is best explained as a relict of *ludoviciana* ssp. *typica* stranded on the western flank of the Sierra Nevada after most of its fellows had been replaced by the younger species, *Douglasiana*. A similar plant from west of Dunlap, Fresno County, *Keck 1861* (CI, SU), may be the same. This suggests that *ludoviciana* ssp. *typica* once skirted the southern end of the Sierra Nevada in a more continuous distribution.

This is probably the most variable systematic unit in the whole complex, as the long synonymy tends to show. Extremes can be pointed out that appear very unlike, but intermediates link all together. This subspecies intergrades not uncommonly with ssp. *candicans* to the northwest, with ssp. *incompta* to the west, and with sspp. *albula* and *mexicana* to the southwest. It does not overlap the ranges of sspp. *sulcata* and *redolens*. Apparently to a much lesser extent it intergrades with *A. serrata, longifolia,* and *Carruthii*.

In the high Rocky Mountains of northern Colorado there is a form that seems to intergrade with the form of *A. Carruthii* known as *A. coloradensis* Osterh. Because it seems impossible to decide from herbarium material whether this is best assigned to *A. Carruthii* as a subspecies, or to *A. ludoviciana* as a subspecies, the question is left open. Perhaps cytological studies will be ultimately decisive, but we have no living material of it. The following specimens are of this intergrading form, all with small deeply divided leaves, the divisions varying from linear to lanceolate: COLORADO. Weld: Windsor, *Osterhout 5041* (RM). Larimer: Pole Hill, *Osterhout 2225* (RM); Cherokee Park, *Nelson 10017* (C, RM); Estes Park, Thompson Canyon, *Johnston 678b* (US). Boulder: Boulder, *Hanson C26* (US). Denver: Denver, *Jones 501c* (Po). Clear Creek: Empire, *Tweedy 5840* (NY, RM); Georgetown, *Shear 4514* (RM); above Silver Dale near Georgetown, July 10, 1878, *Jones* (Po).

6b. **Artemisia ludoviciana** Nutt. ssp. **sulcata** (Rydb.) Keck comb. nov.

Figures 10 and 15

Type locality: Casas Grandes, Chihuahua.

Artemisia sulcata RYDB., N. Amer. Fl. 34:270, 1916.

Stems 3–12 dm. tall, smooth or tomentose, sometimes rather prominently sulcate; leaves lanceolate, sharply acute, the lower tooth apically with short salient lobes, the upper usually entire, reduced in the inflorescence, commonly thin and rather flaccid, mostly 3–10 cm. long and less than 1 cm. wide (exclusive of lobes), usually bright green above, densely white-tomentose beneath, sometimes ± tomentose above, plane; inflorescence a leafy spreading paniele or sometimes reduced and contracted; heads usually distributed in individual nearly naked racemes and pendant; involucre campanulate, 2.5–3 mm. high,

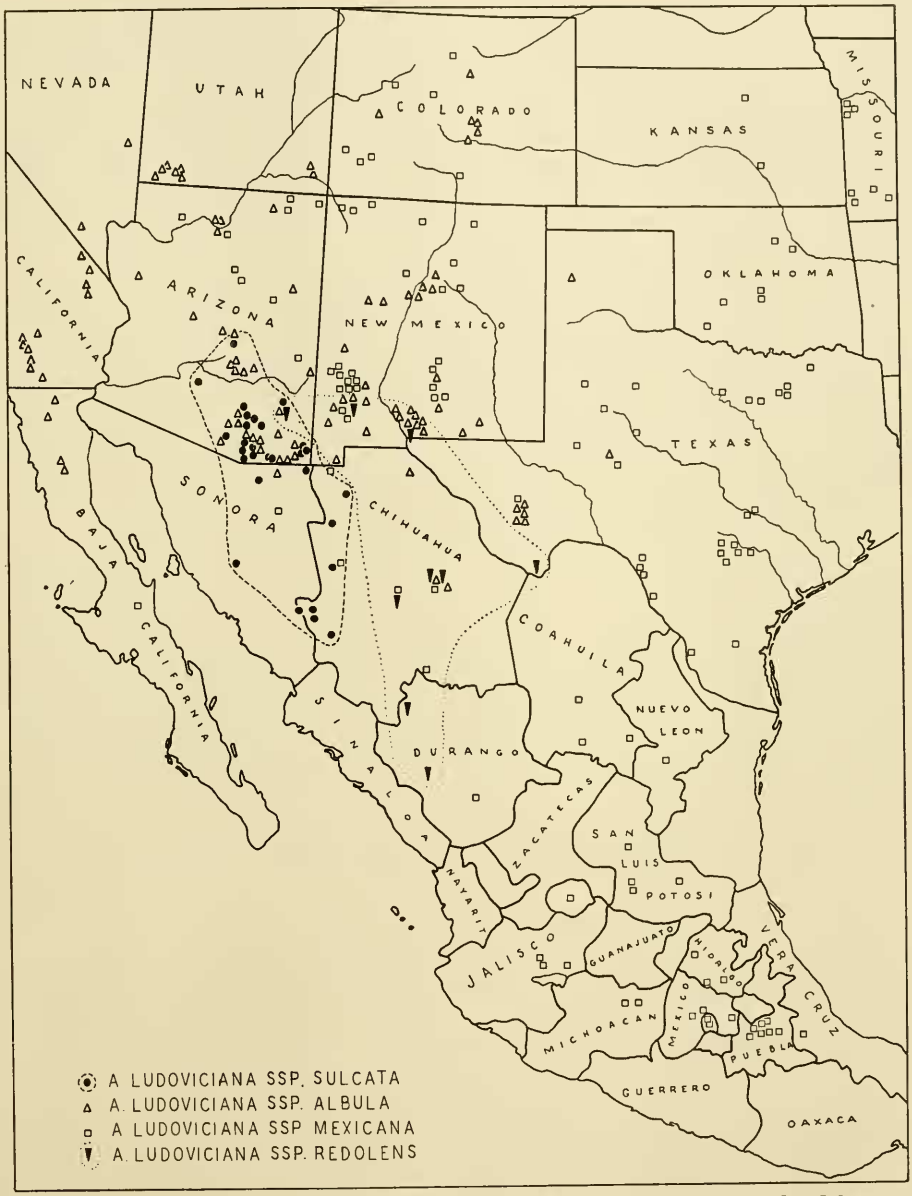


Figure 15. Distribution of *A. ludoviciana* sspp. *sulcata, albula, mexicana,* and *redolens.*

2–3 mm. wide, usually white-tomentose, sometimes quite glabrate (in Chihuahua, as in the type), with 10–16 bracts; ray-florets 6–16; disk-florets 7–19.

High plateaus and mountains from central Arizona to southern Chihuahua, at elevations from 1600 to 2700 m. Flowering from August to October.

ARIZONA. Gila: Upper Tonto Creek, *Harrison and Kearney 8359.* Graham: Mt. Graham, 9000 ft., *Kearney and Peebles 9874.* Pinal: Oracle. Maricopa: Sierra Estrella, *Peebles and*

Kearney 7756. Cochise: between Portal and Paradise; Barfoot Park, *Blumer 1389;* Warren; Mule Mts.; Bisbee; Huachuca Mts., Miller Canyon, *Jones 25073,* Ramsey Canyon, *Shreve 5039.* Pima: Santa Catalina Mts.; Marshall Gulch, *Shreve 5398;* Ft. Lowell, *Thornber 50,* toward ssp. *mexicana;* Baboquivari Canyon; Rincon Mts., Spud Ranch, *Blumer 3594.* Santa Cruz: Santa Rita Mts., *Kearney and Peebles 10569;* Patagonia Mts. SONORA. Cajon Bonito Creek, near its head, *Mearns 2474;* Cananea, *Donnelly 44;* La Mesa Colorado, *Gentry 559.* CHIHUAHUA. Casas Grandes, August 30, 1899, *Townsend and Barber 437* (NY, type; isotype, US; phototype, C); Chuichupa, Sierra Madre, *Townsend and Barber 423;* Colonia Garcia, Sierra Madre, *Townsend and Barber 326;* Norogachi, *E. Palmer S. S.;* Sierra de Papas; San Jose de Pinal, Rio Mayo, *Gentry 2843.*

In proposing *Artemisia sulcata,* Rydberg emphasized the shining glabrate involucres and the grooved stems. As pointed out by Hall and Clements, these do not furnish good criteria for separating *sulcata* from ssp. *mexicana.* Other characters, however, are more dependable for separating these two units, namely, *sulcata* has entire to apically toothed leaves instead of pinnately divided ones, and these are thin and plane instead of thickish and revolute. As shown in the distribution map, figure 15, the range of ssp. *sulcata* is adjacent to that of ssp. *mexicana* which it largely replaces in southern Arizona.

Artemisia ludoviciana ssp. *sulcata* is wedged between sspp. *mexicana, albula,* and *typica.* Intermediates occur between *sulcata* and sspp. *albula* and *mexicana* along the periphery of its range suggesting intercrossing and recombination. Genetic barriers of specific importance have therefore not arisen between these units. Possibly the broader leaves of *sulcata* point to a connection with ssp. *typica.* It appears that ssp. *sulcata* is a recognizable form which may have evolved through the recombination of characters from the three subspecies, *mexicana, albula,* and *typica,* which surround it.

6c. **Artemisia ludoviciana** Nutt. ssp. **albula** (Woot.) Keck comb. nov.

Figures 10 and 15

Type locality: Organ Mountains, New Mexico.

Artemisia microcephala WOOT., Bull. Torr. Club 25:455, 1898; not Hillebr., 1888.

A. albula WOOT., Contr. U. S. Nat. Herb. 16:193, 1913. New name for *A. microcephala* Woot.

Stems 3–10 dm. tall; herbage white-tomentose throughout, rarely the leaves evidently discolored and merely tomentulose on the upper surface; leaves mostly obovate to elliptic, their teeth or lobes projecting forward and not nearly cut to the midrib, the upper ones reduced, often lance-linear and entire, not fascicled, thickish, short (mostly 1–2 cm. long), the margin often narrowly revolute; inflorescence open-paniculate; heads small, racemosely arranged along the elongated divergent remote leafy branchlets, or sometimes ± glomerate; involucre campanulate, *ca.* 3 mm. high, 2 mm. wide, densely tomentose, with 11–16 bracts; ray-florets 8–11; disk-florets 8–13.

Western Texas and southern Colorado to southern Nevada and California, south to northern Baja California, Sonora, and Chihuahua, at elevations from 150 to 2250 m. Flowering from May to October.

Texas. Oldham: Canadian Valley. Jeff Davis: Fort Davis, *Eggleston 17412;* Sawtooth Mt.; Limpia P.O. Colorado. Boulder: Eldorado Springs, *Bartholomew 2* (NY). El Paso: Bear Creek Canyon. Fremont: Canon City, *Biltmore 1437a.* Delta: Paonia, *Eggleston 14954.* New Mexico. Sandoval: Sandia Mts., *Eastwood 15650.* Bernalillo: Albuquerque. Valencia: Laguna. Catron: Mangas. Lincoln: Gray, *Earle 457.* Sierra: Hillsboro, *Metcalfe 1445.* Grant: Bear Mt., *Metcalfe 709.* Eddy: Carlsbad Caverns. Dona Ana: Organ Mts., 4500 ft., Sept. 1, 1897, *Wooton 504* (US, type; phototypes, C, NY, US; isotypes, NY, US). Luna: Florida Mts. Hidalgo: Lordsburg; Dog Spring, *Mearns 2370.* Utah. San Juan: Butler Wash; Bluff. Washington: Zion National Park; St. George. Nevada. Lincoln: Panaca. Clark: Charleston Mts., *Coville and Funston 372.* Arizona. Apache: Petrified Forest N. of Adamana. *Hall 11171.* Navajo: Shonto. Coconino: Grand Canyon, *Eastwood and Howell 7006.* Mohave: White Cliffs E. of Kingman. Yavapai: Weaver Mts., *Gillespie 8498.* Gila: Payson; Globe. Maricopa: Fish Creek. Pinal: Superstition Mt., *Gillespie 8585.* Greenlee: Blue River. Graham: Ft. Grant. Cochise: Paradise, *Blumer 1798;* Dragoon Pass, *Jones 28623;* Bisbee. Pima: Tucson; Baboquivari Canyon. California. Tulare: Kern River at Funston Creek, 6900 ft., *Sharsmith 3840.* San Bernardino: Clark Mt.; 5 mi. S. of Barnwell, *Munz 13838;* Providence Mts.; Little San Bernardino Mts. Riverside: Tahquitz Canyon, Palm Springs, *Wheeler 2296;* San Jacinto River Canyon. San Diego: Borrego Valley. Chihuahua. Candelaria, *Stearns 276;* Sierra en Media, *E. W. Nelson 6488;* Santa Eulalia Mts., *Pringle 626.* Sonora. San Jose Mts., *Mearns 1055.* Baja California. Cantillas Mts., 1875, *E. Palmer;* between Ojos Negros and Neji Rancho, *Wiggins and Gillespie 4146;* La Encantada, Sierra San Pedro Martir, *Wiggins and Demaree 4877, 4999* (Po, SU, both atypical, toward ssp. *sulcata* or *mexicana*).

Hall and Clements included this form under *A. vulgaris* ssp. *gnaphalodes,* although they accurately pointed out its outstanding characteristics. Blake, in Kearney and Peebles' Flowering Plants and Ferns of Arizona, likewise refers it to *A. gnaphalodes.* It will be seen from the distribution map that as here circumscribed *A. ludoviciana* ssp. *typica* (which includes *A. gnaphalodes*) and *A. ludoviciana* ssp. *albula* largely occupy different geographical areas. Their different morphological patterns mark them as excellent examples of geographical subspecies.

6d. **Artemisia ludoviciana** Nutt. ssp. **candicans** (Rydb.) Keck comb. nov.

Figures 10 and 16

Type locality: Little Belt Mountains, Montana.

Artemisia ludoviciana var. *latiloba* Nutt., Trans. Amer. Phil. Soc. II, 7:400, 1841. "With the above [*A. ludoviciana*], in the Rocky Mountains." According to Rydberg, the same as his *A. platyphylla,* but the entity uncertain, with no type found.

A. candicans Rydb., Bull. Torr. Club 24:296, 1897.

A. floccosa Rydb., *ibid.* 297. In the type of *candicans* the heads are sessile along the branchlets of the inflorescence and thus rather glomerate; in the type of *floccosa* the heads are short-pediceled and arranged in a long spike-like panicle. In other respects the two forms are closely similar. Type locality: Lima, Montana.

A. paucicephala A. Nels., Bull. Torr. Club 27:35, Jan. 24, 1900. A form with many of the leaves entire and thus allied to ssp. *typica;* however, some leaves are deeply parted, and the very large heads ally it more closely to this than to *typica.* Type locality: near Yellowstone Lake on the banks of a tributary creek.

A. gracilenta A. Nels., *ibid.* A foliage form of the preceding, with the leaves twice cut and the lobes more slender, in this respect comparable with the *Flodmanii* form of ssp. *incompta.* Type locality: sandy beaches and banks of Yellowstone Lake.

Figure 16. Distribution of *A. ludoviciana* sspp. *candicans* and *incompta*.

A. latiloba RYDB., Mem. N. Y. Bot. Gard. 1:429, Feb. 15, 1900.

A. platyphylla RYDB., N. Amer. Fl. 34:275, 1916. Leaves of the type large and cut much like those of *A. Douglasiana*, that is, cuneate-obovate and toothed or short-lobed toward apex, but the inflorescence and pubescence are like *candicans*. Furthermore, a large series of variations from the Spokane region in the Herbarium of the University of California make the complete transition to *candicans*. Ssp. *typica* is not only very rare in Washington, but has much smaller heads than this. Although chromosome counts

are lacking which would clinch the matter, we suspect *A. Douglasiana* may occur in this region, but in an atypically gray-pubescent form. The type locality of *A. platyphylla* is sandy or gravelly banks of Spokane River, Spokane, Washington.

A. vulgaris ssp. *candicans* Hall et Clem., Carn. Inst. Wash. Publ. 326:73, 1923.

A. vulgaris var. *candicans* Peck, Man. Higher Pl. Ore. 766, 1941.

Stems 3–10 dm. tall, entirely herbaceous; herbage white-tomentose throughout; leaves oblanceolate to broadly elliptic in outline, deeply pinnately cleft or parted into forward-projecting narrow lobes, at least some lobes again toothed, or sometimes the leaves merely pinnately lobed and the upper ones entire, 5–10 cm. long, 1.5–4 cm. wide, sometimes more thinly tomentose on upper surface, but rarely ever green, plane or nearly so; inflorescence a somewhat leafy narrow panicle, the heads borne singly or in small glomerules, large, sometimes nodding; involucre broadly campanulate to hemispheric, 3.5–4 mm. high, 3–7 mm. wide, tomentose, with 9–14 bracts; ray-florets 7–12; disk-florets 17–42.

Lowlands and mountains up to middle elevations (2400 m.) from western Montana and Wyoming to northern Utah and westward to central Washington, Oregon, and northern California. Flowering from June to September.

Montana. Glacier National Park: Baring Basin, *Standley 17159*. Flathead: Summit; Belton. Judith Basin: Little Belt Mts., 6 mi. from Barker, 6000 ft., Aug. 18, 1896, *J. H. Flodman 882* (NY, type of *A. candicans;* isotype, US). Gallatin: Sedan. Beaverhead: Lima, Aug. 6, 1895, *Rydberg 2942* (NY, type of *A. floccosa;* isotype, US). Park: Gardiner, *Hawkins 728a*. Wyoming. Yellowstone National Park: Yellowstone Lake, Aug. 22, 1899, *A. and E. Nelson 6612* (RM, type of *A. gracilenta;* isotypes, NY, RM), ditto, Aug. 6, 1899, *A. and E. Nelson 6344* (RM, type of *A. paucicephala;* isotypes, NY, Po, RM, SU). Teton: Teton Forest Reservation, *Brandegee*. Sweetwater: 6 mi. N. of Rock Springs. Uinta: West Fork of Bear River, *Payson 4840*. Utah. Cache: Summer Camp, Logan Canyon, *Art Smith*. Idaho. Bonner: Lake Pend d'Oreille. Kootenai: Farmington Landing, *Sandberg et al. 569;* Couer d'Alene, *Leiberg 1552*. Latah: Comerine Gulch. Lemhi: Gilmore. Fremont: St. Anthony. Blaine: Hailey. Custer: Alturas Inlet. Washington: Tamarack, *Clark 227*. Owyhee: Twilight Gulch, *Macbride 486*. Nevada. Elko: Little Lakes Canyon. White Pine: Duck Creek, Ely, *Mitchcock 1390*. Humboldt: Winnemucca, *Griffiths and Morris 40*. Washington. Spokane: banks of Spokane River, Spokane, June 1897, *Elmer 867* (NY, type of *A. platyphylla;* isotypes, Po, US), ditto, Oct. 1921, *Moore* (C, a large series of variations). Whitman: S.E. of Lamont; Wawawai, *Keck 382*. Columbia: Blue Mts. Adams: Sheep Springs, *Leiberg 944*. Grant: Soap Lake, *Thompson 11795*. Chelan: Mt. Stuart. Kittitas: Ellensburg. Yakima: Upper Naches River. Oregon. Wallowa: Joseph; Wallowa Lake. Union: La Grande. Umatilla: Toll Gate. Hood River: Hood River. Grant: Izee. Crook: Prineville. Lake: Silver Lake, *Leiberg 758*. Klamath: Pelican Bay. California. Modoc: Lily Lake, Pine Creek. Nevada: ridge S. of Donner Pass, 8500 ft., *Heller 7153*.

This subspecies occurs through approximately the same geographical region as ssp. *incompta*, but for the most part at lower elevations and in a different life zone. Transitional specimens are not infrequently found between these two subspecies. Likewise, transitions are sometimes found between ssp. *candicans* and ssp. *typica*. As mentioned under the synonym *A. platyphylla*, forms from Washington are sometimes difficult to separate from *A. Douglasiana*, although presumably the two have a genetic barrier to their interbreeding in

a difference in chromosome number. It is quite possible that the *Douglasiana*-like forms of *candicans* have arisen independently as a parallel variation and are not the result of *Douglasiana* genes picked up through crossing. This possibility gains credence from the complete series of intermediates linking these broad-leaved forms with the narrow-leaved forms of *candicans*.

6e. **Artemisia ludoviciana** Nutt. ssp. **incompta** (Nutt.) Keck, Carn. Inst. Wash. Publ. 520:327, 1940.

Figures 8, 10, and 16

Type statement: "In the central chain of the Rocky Mountains, in Thornberg's Pass, near the great passage to the plains of the Oregon." This locality is in Custer County, Idaho, and the type was collected by Nuttall.

Artemisia incompta NUTT., Trans. Amer. Phil. Soc. II, 7:400, 1841.

A. discolor var. *incompta* GRAY, Syn. Fl. 1(2):373, 1884.

A. atomifera PIPER, Contr. U.S. Nat. Herb. 11:588, 1906. A form from Wawawai, Washington, on the Snake River, with thick, strongly discolored leaves that are green on the upper surface, and some of which are bipinnately lobed. An unusual variant from within the zone of *candicans*, but from its morphology best assigned to *incompta*. Wide variation is exhibited at the type locality, so it is impossible to distinguish a separate systematic unit here.

A. ludoviciana var. *atomifera* M. E. JONES, Bull. Univ. Mont. Biol. ser. 15:48, 1910.

A. potens A. NELS., Bot. Gaz. 54:418, 1912. A greenish form very similar to the type of *incompta* taken not far from the type locality of this subspecies. Type locality: Mackay (Pass Creek), Custer Co., Idaho.

A. Flodmanii RYDB., N. Amer. Fl. 34:276, 1916. A densely tomentose form with linear divisions to the leaves; heads medium-sized, too small for *candicans*. An uncommon form, but principally found in western Montana. Type locality: Little Belt Mountains, Montana, 9 miles east of Barker.

A. vulgaris ssp. *Flodmanii* HALL et CLEM., Carn. Inst. Wash. Publ. 326:75, 1923.

A. vulgaris ssp. *Michauxiana* var. *incompta* ST. JOHN, Res. Stud. St. Coll. Wash. 1:106, 1929.

A. vulgaris var. *Flodmanii* PECK, Man. Higher Pls. Ore. 767, 1941.

Stems 3–9 dm. tall, usually entirely herbaceous; herbage commonly ± green, with leaves glabrate above and white-tomentose beneath, but often ± densely tomentose throughout, and sometimes essentially glabrous throughout; lower leaves mostly obovate to broadly elliptic in outline, rarely fascicled, parted or divided into linear or lanceolate often elongated forward-projecting lobes, some of these again toothed or lobed, 2–8 cm. long, the upper leaves less cut or even entire, the margin rarely revolute; inflorescence a narrow spike-like or even racemose panicle, sometimes much broader but not open, not very leafy; heads rather large, nodding at first or erect; involucre broadly campanulate, 3–3.5 mm. high, 2.5–4 mm. wide, sericeous-tomentose to glabrate and shining, with 9–14 bracts; ray-florets 6–10; disk-florets 15–30(–45). $n = 18$.

Mountains of Montana and Idaho, southward to central Utah, Nevada and California, at elevations from 1400 to 3000 (to 3500) m. Flowering from July through September.

MONTANA. Glacier: Swiftcurrent Creek, *Standley 16071.* Cascade: Belt Creek. Judith Basin: Little Belt Mts., 9 mi. from Barker, Aug. 18, 1896, 6,000 ft., *Flodman 883* (NY, type of *A. Flodmanii;* isotype, US). Sweet Grass: Sweet Grass Canyon, Crazy Mts. Lewis and Clark: Gate of the Mountains. Jefferson: Boulder Creek. Silver Bow: Durant. Gallatin: Bridger Mts., Aug. 21, 1902, *W. W. Jones.* Park: Emigrant Gulch, *Rydberg and Bessey 5206.* Beaverhead: Lima, *Shear 5062.* WYOMING. Yellowstone National Park: Madison River. Teton: Government Bridge; Jackson Hole, *Payson 2264.* Lincoln: Salt River Mts. E. of Smoot. Carbon: Bridger Peak. COLORADO. Routt: Anita Peak, *Goodding 1753.* Eagle: Red Cliff. UTAH. Cache: Tony Lake basin, *Maguire 16105.* Salt Lake: Alta. Utah: Mt. Timpanogas. Juab: Mt. Nebo. San Pete: Reeder Canyon. Sevier: Fish Lake (C); head of Bullion Creek, 11,500 ft., *Jones 5873.* IDAHO. Lemhi: Gilmore, *Hall 11552.* Custer: Garden Creek, near Challis, *Macbride and Payson 3350;* Mackay, Pass Creek, 6,700 ft., July 30, 1911, *Nelson and Macbride 1413* (RM, type of *A. potens;* isotypes, C, NY, Po, SU, US); Mackay, Bear Canyon, *Nelson and Macbride 1521;* Thornberg's Pass, *Nuttall* (Ph, type of *A. incompta*). Blaine: Alturas Lake; Ketchum. Owyhee: Twilight Gulch, *Macbride 485.* NEVADA. Elko: Coon Creek, Jarbidge Mts. (SU); Spruce Mt.; Lamoille Canyon. White Pine. Sherman Peak, Ruby Mts., *Hitchcock and Martin 5651.* Pershing: Star Peak, *Watson 638.* Lander: 35 mi. S.W. of Austin; W. of Bunkerhill Mt. Humboldt: Winnemucca; Humboldt Canyon, *Heller 10625.* Washoe: Galena Creek; Mt. Rose. Mineral: Walker Lake, *Tidestrom 10157.* Clark: Rainbow Falls, Charleston Mts., *Clokey 7388.* WASHINGTON. Whitman: Wawawai, Sept. 1903, *C. V. Piper 6466* (US, type of *A. atomifera;* isotypes, CAS, NY, SU, US). OREGON. Wallowa Lake; Bear Creek, *Sheldon 8809;* West Fork, Wallowa River, *Keck 366.* Grant: Strawberry Mt. Harney: base of Steins Mts. CALIFORNIA. Modoc: Cedar Mt. Lassen: Janesville. Plumas: Prattville. Nevada: Soda Springs. Placer: Summit, *Heller 12898.* Alpine: Ebbet Pass; Sonora Pass. Mono: Blue Lake; Leevining Grade, *Keck 5015;* McAfee Meadows, White Mts., 11,500 ft., *Duran 2834* (C, SU, with small finely cut leaves like the *tenuis* form of *A. Michauxiana*). Tuolumne: Upper Relief Valley; Tuolumne Meadows. Mariposa: Washburn Lake. Madera: Merced Pass, *Bolander 6152.* Inyo: Piute Pass-North Lake Trail, *Ferris 8937;* Mt. Baxter. Tulare: Kaweah Peaks; trail to Mt. Whitney, *Culbertson in Baker 4341;* Little Kern; Junction Meadows. Los Angeles: Swartout Valley, *Munz 7711;* Pine Mt. ridge, *Johnston 1651.* San Bernardino: Vivian Creek; Big Meadows of Santa Ana; Dry Lake, Mt. San Gorgonio. Riverside: Strawberry Valley, San Jacinto Mts., *Wheeler 171.*

Chromosomes were counted in meiotic divisions of two plants from Yosemite Creek, Tioga Road, Yosemite National Park, at 2200 m. elevation, and in somatic divisions in root-tips of a plant from White Mountain, Yosemite National Park, at 3200 m., and of another from Slate Creek Valley, Mono County, California, at 3260 m. elevation. An additional plant from Slate Creek Valley proved to be hexaploid, with $2n = ca.$ 54. (See Clausen, Keck, and Hiesey, 1940a, p. 336, for additional information on this plant.)

As is the case with most of the other units in this complex, ssp. *incompta* is extremely variable, and many collections included here neither fully fit the description nor bear a close resemblance to even neighboring collections. The closest resemblance of ssp. *incompta* within the species is to *typica* and *candicans.* Intergrades are not rare. As shown in the map, figure 16, ssp. *incompta* ranges farther south than ssp. *candicans.* The exact boundaries cannot be automatically determined. For instance, on the higher summits of the Wasatch Range in San Pete County, Utah, far south of the range of typical *candicans,* four collections have been studied all of which bear a morphological resem-

blance to *candicans*, but which might be classed as intermediates. From their occurrence well within the region of *incompta* and their transitional appearance, these are considered an example of parallel variation within *incompta* rather than representatives of *candicans* of disjunct distribution.

The relationships of ssp. *incompta* outside the species are with *A. Michauxiana* and *Lindleyana*. This is suggested, also, in figure 19, page 466. The breaks between these units, however, seem to be more clear cut than those between the subspecies of *ludoviciana*, and this helps justify the maintenance of species instead of subspecies. A thorough cytological survey should precede drastic taxonomic shifts in this group.

6f. **Artemisia ludoviciana** Nutt. subsp. **mexicana** (Willd.) Keek comb. nov.

Figures 10 and 15

Type locality: Mexico. Type not seen.

Artemisia mexicana WILLD. in Spreng., Syst. 3:490, 1826.

Oligosporus mexicanus LESS., Syn. Gen. Compos. 264, 1832.

Artemisia indica mexicana BESS., Nouv. Mém. Soc. Nat. Mosc. 3:56, 1834.

A. vulgaris var. *mexicana* TORR. et GRAY, Fl. N. Amer. 2:421, 1843.

A. cuneifolia SCHEELE, Linnaea 22:162, 1849. Type not seen, but according to Hall and Clements this is a tall, very erect and rigid, small-headed form of the subspecies here considered. Type locality: high places on the prairie near New Braunfels, Texas.

A. Lindheimeriana SCHEELE, *ibid.* 163. Type not seen, but according to Hall and Clements stems rigid and almost woody; heads only 2 mm. across. Type locality: in the dry river bed of the Cibolo, fifteen miles west of New Braunfels, Texas.

A. Underwoodii RYDB., Bull. Torr. Club 32:129, 1905. A form with the deeply lobed, strongly discolored foliage of *mexicana* and the compact spike-like panicle of *typica*, to which it is rather intermediate. Type locality: Ouray, Colorado.

A. revoluta RYDB., N. Amer. Fl. 34:272, 1916. Form with very narrow, elongated, revolute divisions of the leaves and a narrow inflorescence. Type locality: city of Chihuahua.

A. texana RYDB., *ibid.* 274. Intermediate to *typica*, with broad leaves, the upper of which are entire. Judging from its distribution and the presence of intergrades, a tomentose form of *mexicana*. Type locality: Colorado, Texas.

A. Ghiesbreghtii RYDB., *ibid.* 271. An exceptionally large-headed form of *mexicana*, but lacking the type of *mexicana*, and finding head size a variable character in Mexico, it seems best to put this into synonymy here. Type locality: Chiapas.

A. Muelleri RYDB., *ibid.* 270. A form with rather wide mostly entire upper leaves. Type locality: Orizaba.

A. neomexicana GREENE ex RYDB., *ibid.* 279. A narrow-leaved form approaching *A. Carruthii*, strongly discolored; inflorescence rather narrow for the subspecies. Type locality: in a grassy glade, Hillsboro Peak, Black Range, New Mexico.

A. vulgaris ssp. *mexicana* HALL et CLEM., Carn. Inst. Wash. Publ. 326:80, 1923.

A. ludoviciana Lindheimeriana BUSH, Amer. Midl. Nat. 11:35, 1928.

A. ludoviciana var. *mexicana* FERN., Rhodora 47:248, 1945.

Stems 3–10 dm. tall, densely leafy, herbaceous to base; leaves variable, typically 5–10 cm. long, with few linear pinnate spreading entire divisions 2–4 mm. wide, but the upper and many of the cauline often entire or nearly so, and the lower cauline often merely ternately divided, loosely floccose to glabrous and dark green above, densely white-tomentose beneath, often thickish, nar-

rowly revolute; inflorescence a rather dense leafy branching panicle 3–10 cm. broad; heads rather small, erect or more commonly nodding; involucre turbinate to campanulate or hemispheric, 2.5–3.5 mm. high, 2–3 mm. wide, sparingly to densely tomentose, with 10–15 bracts; ray-florets 5–12; disk-florets, 6–18.

Western Missouri to Colorado, Arizona, and southward to Guatemala, at elevations from 250 to 3050 m. Flowering from August through October. Type locality: Mexico.

Missouri. Jackson: Courtney, *Bush 6509*. Greene: Springfield, *Standley 8637*. Arkansas. Pulaski: Little Rock, Sept. 1886, *Hasse* (SU). Kansas. Cloud: Aurora, *Fraser 553*. Sedgwick: Wichita. Oklahoma. Creek, Payne, Cleveland, Caddo, and Kiowa counties. Texas. Fannin, Dallas, Tarrant, Parker, Young, Dickens, Lubbock, Garza, Midland, Tom Green, Jeff Davis, Travis, Kendall, Comal, Bexar, Valverde, Maverick, Webb, and Duval counties. Mitchell: Colorado, *Tracy 8141* (NY, type of *A. texana;* isotypes, NY, US). Colorado. Larimer: Moraine Park, *Osterhout 3130* (RM, atypical). Summit: Breckenridge, *Mackenzie 237* (NY, atypical). Garfield: Glenwood Springs, *Osterhout 3309* (RM, atypical). Ouray: chaparral covered hills S.E. of Ouray, *Underwood and Selby 74* (NY, type of *A. Underwoodii;* phototype, C). Montrose: Naturita, *Payson 590*. San Miguel: Telluride, 10,000 ft., *Tweedy 332*. New Mexico. Colfax, Rio Arriba, San Juan, Sandoval, Lincoln, Otero, Catron, and Sierra counties. Grant: Hillsboro Peak, Black Range, *Metcalfe 1248* (NY, type of *A. neomexicana;* phototype, C; isotypes, CAS, Po, RM, US). Arizona. Apache: Carrizo Mts.; Hannagan Meadow, White Mts., 1935, *McNeill*. Navajo: Kayenta; Holbrook. Coconino: Grand View, Grand Canyon, *Eastwood 3611* (CAS, toward *albula*); S. of Flagstaff. Sonora. Halfway between Cumpas and Baviacora, *Drouet et al. 3654*. Chihuahua. Boundary, near White Water, *Mearns 2281;* Soldier Canyon, Sierra Madre; Colonia Garcia, *Townsend and Barber 296;* by streams near Chihuahua, *Pringle 290* (NY, type of *A. revoluta;* phototype, C; isotypes, NY, Ph); between Porral and San Julian, *E. W. Nelson 4939* (US, toward *redolens*). Coahuila. Soledad, *E. Palmer 736* (toward *albula*); Sierra de Parras, *Purpus 4659* (toward *Carruthii*); Saltillo, *E. Palmer 286* (possibly a distinct subspecies, with broad, venulose, involute-margined, tomentose leaves like some Texan forms but showing some characters of *typica*). Nuevo Leon. Galeana, *Taylor 207*. Durango. Durango, *E. Palmer 600, 601, 602, 907*. San Luis Potosi. Alvarez, *E. Palmer 59;* San Luis Potosi, *Parry and Palmer, 530, 531*. Aguascalientes. Aguascalientes, *Rose and Painter 7760*. Jalisco. Rio Blanco; Guadalajara, *Pringle 8765*. Hidalgo. Dublan; Pachuca; Tula, *Pringle 9848*. Mexico. Contadero; Eslava. Federal District. Mexico City. Michoacan. Morelia. Vera Cruz. Orizaba, *Fred Müller 235* (NY, type and isotype of *A. Muelleri*) Puebla. Puebla. Chiapas. Without exact locality, *Ghiesbrecht 155* (NY, type of *A. Ghiesbreghtii*, the spelling inadvertently (?) altered by Rydberg). Guatemalia. San Pedro S., *Tejada 49* (US). Apparently introduced and cultivated in San Salvador, *Calderon 2255* (US), where the collector reports it to be "much used by native people as remedy for various affections."

At least as variable a subspecies as *typica*, but difficult to subdivide further on the basis of present collections. Undoubtedly distinct ecotypes remain to be worked out in the Mexican highlands. A few forms, now puzzling, await a fuller understanding before adequate treatment. For example, a collection from San Pablo, Baja California, collected April 21, 1889, by T. S. Brandegee (C), from well outside the range of this otherwise fall flowering subspecies, is best referred here temporarily on the basis of form. Intergrades link ssp. *mexicana* with ssp. *typica*, *albula*, and *redolens*.

6g. **Artemisia ludoviciana** Nutt. ssp. **redolens** (Gray) Keck comb. nov.
Figures 10 and 15

Type statement: "Chihuahua, on cool slopes under cliffs, *Pringle*, 296."

Artemisia redolens GRAY, Proc. Amer. Acad. 21:393, 1886.
A. vulgaris ssp. *redolens* HALL et CLEM., Carn. Inst. Wash. Publ. 326:75, 1923.

Stems 4–8 dm. tall; herbage quite glabrous throughout and glandular-atomiferous to moderately tomentose, especially on under surfaces of leaves; leaves broadly ovate in outline, the lower bipinnately dissected, the salient lobes rather narrow and short (mostly less than 1 cm. long), 2–5 cm. long, nearly as wide, the upper toothed to entire, narrowly linear, the margin sometimes narrowly revolute; inflorescence a broad leafy panicle with ascending branches bearing small usually erect heads in delicate racemes; involucre broadly campanulate, 2.5–3 mm. high, 3 mm. wide, sparingly silky tomentose, with 12–14 bracts; ray-florets 6–10; disk-florets 8–14.

Westernmost Texas, southern New Mexico and southeastern Arizona (in somewhat atypical form) to Chihuahua and Durango, at elevations from 1800 to 2500 m.

TEXAS. Brewster: Chisos Mts., *Mueller 8242*. NEW MEXICO. Dona Ana: Organ Mts., Sept. 23, 1906, *Wooton and Standley*. Grant: Copper Mines (Santa Rita), *Wright 1278*, in part (Ph). ARIZONA. Graham: Mt. Graham, 7500 ft., *Kearney and Peebles 9796* (possibly a form of *A. Carruthii*). CHIHUAHUA. In shade of cliffs, rocky hills near Chihuahua, *Pringle 296* (Gray, type; isotypes, NY, Ph, US), *1059;* Soldier Canyon, Sierra Madre, *Jones*. DURANGO. San Julian to Cerro Prieto, *E. W. Nelson 4956;* Sandia Station, *Pringle 13535*.

This unit is somewhat variable and its distribution is within the region occupied by ssp. *mexicana*. However, the distinctive foliage and sparse pubescence serve to distinguish it from *mexicana*, so that it appears to be quite apart. A very few intermediates are found. The lower leaves of spp. *redolens* are bipinnately dissected like those in *A. Michauxiana*, a form very different otherwise and from an entirely different habitat in the northern Rockies, but the correspondence in leaves is suggestive. Possibly each of these units will prove to have a different chromosome number from *A. ludoviciana*, and each may have had a long independent history behind it.

7. **Artemisia Lindleyana** Bess. in Hook., Fl. Bor. Amer. 1:322, 1833.
Figures 10 and 17

Type statement: "North-West coast of America. *Douglas*, in *Herb. Lindl. n.* 16." The following three collections in the Kew Herbarium, collected by David Douglas, may include an isotype of the species: abundantly on the sands of the seashore near the straits of Juan de Fuca, 1825, *Douglas* (Hb. Benth., I doubt the locality on this label); in the channels of mountain streams near the sources of the Columbia, common, *Douglas* (possibly a part of the previous collection, in which case these data as to the source are probably correct); Columbia River, 1830, *Douglas*.

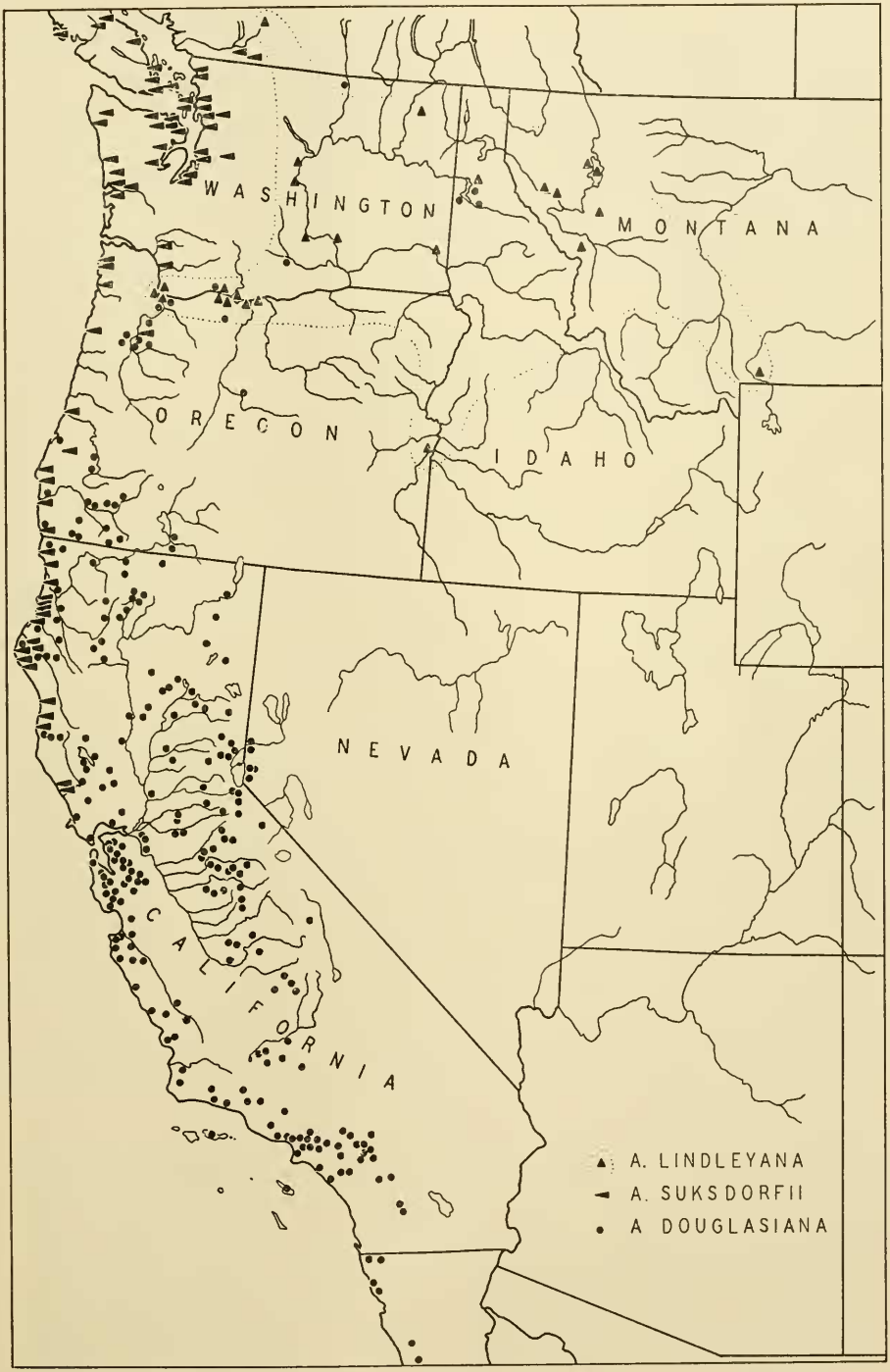


Figure 17. Distribution of *Artemisia Lindleyana*, *A. Suksdorfii*, and *A. Douglasiana*.

Artemisia Lindleyana α legitima BESS., *ibid.* "Folia integerrima 1–1½ longa, vix ⅛ lata." By inference, Douglas no. 16.

A. Lindleyana β brevifolia BESS., *ibid.* "Fors status serotinus: nam adsunt tantum folia fasciculorum unguicularia." By inference, Douglas no. 14.

A. Lindleyana γ subdentata BESS., *ibid.* "Folis versus apicem uno alterne 1–½" [half inches] longa, 1–2‴ [lines] lata." By inference, Douglas no. 18.

A. Lindleyana δ Coronopus BESS., *ibid.* "Folia *Plantaginis Coronopi.*" These varieties are leaf variations that appear to have no ecotypical value.

A. pumila NUTT., Trans. Amer. Phil. Soc. II. 7:399, 1841: not Link, 1822. A starred specimen labeled in Nuttall's hand "Artemisia *pumila. R. Mts. U. Calif." seen in Philadelphia Academy.

A. tenuis var. *integerrima* RYDB., Mem. N. Y. Bot. Gard. 1:432, 1900. Lower leaves missing but upper ones entire, green, very lightly villous on under surface; herbage glandular; stems glabrate, sulcate. Assigned to this species somewhat doubtfully. Type locality: Emigrant Gulch, Park Co., Montana.

A. arachnoidea SHELD., Bull. Torr. Club 30:310, 1903. Leaves linear-lanceolate, tapering to base and apex, very green, but somewhat tomentose beneath. A wide-leaved form of this, rather than of *A. Douglasiana* to which it was assigned by Hall and Clements (under the name *A. vulgaris* ssp. *heterophylla*). Type locality: sandy banks of the Columbia River, 1 mile west of Vancouver, Washington.

A. Leibergii RYDB., N. Amer. Fl. 34:267, 1916. Leaves narrow in type specimen, remotely but sharply toothed apically, nearly glabrous. Type locality: Fish Hook Ferry, Adams Co., Washington.

A. vulgaris ssp. *Lindleyana* HALL et CLEM., Carn. Inst. Wash. Publ. 326:79, 1923.

A. vulgaris var. *Lindleyana* JEPS., Man. Fl. Pl. Calif. 1142, 1925.

Chamaephyte; stems 2–4 dm. tall, several from a woody base; basal leaves linear-oblanceolate (rarely spatulate or wider), entire to serrate-dentate apically or more deeply lobed, often crowded, with fascicles developing in their axils, the upper mostly entire, 2–5 cm. long, mostly less than 1 cm. wide, tomentulose throughout, or more commonly green and glabrate above, white-tomentose beneath; inflorescence a racemose or spike-like panicle, usually narrow and short, 1–2 cm. wide; involucre campanulate, 3 mm. high, 2–3 mm. wide, usually lightly tomentulose, with 9–13 bracts; ray-florets 5–9; disk-florets 10–30.

Drainage of the Columbia River, mostly along the banks of this stream and its tributaries, from western Montana and southern British Columbia to Washington and Oregon; mostly from low elevations, but ascending to 1980 m. in Montana. Flowering from July through September.

BRITISH COLUMBIA. Yale: Siemamous, July 3, 1889, *Macoun* (NY, doubtfully referred here). New Westminster: Fort Hope, *Howell 7766.* MONTANA. Flathead: Flathead Lake. Sanders: Weeksville, *Leiberg 1567;* Plains, *Kirkwood 2510.* Lake: St. Ignatius, Mission Mts., *Kirkwood 1347.* Missoula: Monture Trail. Park: Emigrant Gulch, Aug. 23, 1897, 6500 ft., *Rydberg and Bessey 5201a* (NY, type of *A. tenuis* var. *integerrima;* isotype, US). IDAHO. Kootenai: near Thompson Mt., *Leiberg 1610.* WASHINGTON. Stevens: Old Ft. Colville. Whitman: Wawawai. Franklin: Fish Hook Ferry, *Leiberg 935* (NY, type of *A. Leibergii;* phototype, C; isotype, US), *934, 936, 937.* Chelan: Entiat; Wenatchee. Yakima: Priest Rapids. Klickitat: Grand Dalles, *Keek 341.* Clark: Vancouver, Aug. 31, 1902, *Sheldon S. 11284* (NY, type of *A. arachnoidea;* isotypes, Po, US). OREGON. Malheur: 3 mi. N. of

Adrian, *Peck 16070*. Sherman: Biggs, *Hall 11638*. Wasco: mouth of Deschutes River. Hood River: Hood River. Multnomah: Hayden Island.

This species has not been well understood. Attention has been focused only on traditional taxonomic characters, and little attention has been paid to its distribution and ecologic connections. As a result an unnatural assemblage of plants, distributed very disruptedly over most of the western states and having superficial similarities in leaves and inflorescence, has been assembled under this name. For these reasons it was not discovered that *A. Lindleyana* is a suffrutescent, narrow-leaved species, that follows the banks of the Columbia River and its tributaries.

The nearest connections of *Lindleyana* appear to be with sspp. *incompta* and *typica* of tetraploid *ludoviciana,* but possibly a close relationship can be demonstrated between it and hexaploid *Douglasiana*.

8. **Artemisia Suksdorfii** Piper, Bull. Torr. Club 28:42, 1901.

Figures 3, 10, and 17

Type locality: Stony sea-beaches near Fairhaven, Washington.

Artemisia heterophylla Nutt., Trans. Amer. Phil. Soc. II, 7:400, 1841, in part; not Bess., 1834.

A. vulgaris var. *litoralis* Suksd., Deutsch. Bot. Monatschr. 18:98, 1900. This and *A. Suksdorfii* are based upon the same type collection.

A. vulgaris ssp. *litoralis* Hall et Clem., Carn. Inst. Wash. Publ. 326:76, 1923.

Stems 6–12(–15) dm. tall, stout, herbaceous, or somewhat suffrutescent at base; leaves all broadly lanceolate to elliptic, tapering to base and apex, or some broadly oblanceolate and merely obtuse at apex, entire or with a few coarse teeth or short lobes, gradually reduced within inflorescence, 8–15 cm. long, 1.5–3 cm. wide, all strongly discolored, bright deep green and glabrous or sparsely tomentulose above, silvery tomentose beneath, usually plane; inflorescence a very dense terete or narrowly ovoid leafy panicle, 4–10 cm. broad; heads small, commonly erect; involucre terete or narrowly ovoid, 3–4 mm. high, less than 2 mm. wide, slightly tomentulose or glabrate, yellow-green and shining, with 6–9 bracts; ray-florets 3–7; disk-florets 2–8. $n = 9$.

Vancouver Island southward to Sonoma County, California, in the immediate vicinity of the coast, following a few of the rivers a short distance inland, apparently not ascending more than 100 m. above sea-level.

British Columbia. Westminster: Chilliwack Valley, *Macoun 26352*. Nanaimo: Qualicum; Alberni Canal; Ucluelet. Victoria: Sidney; Victoria. Washington. Whatcom: Chuckanut Bay, *Suksdorf 980* (C, NY, US, isotypes). San Juan: Kanaka Bay, *Zeller 909*. Snohomish: Dean Creek, S. of White Horse, *Keck 5205*. Clallam: Sequim; Olympic Mts., *Elmer 2603;* Beaver; Mora. Jefferson: Duckabush. King: Seattle; E. of Scenic. Mason: Hoodsport. Pierce: Steilacoom. Grays Harbor: Montesano, *Heller 3976*. Cowlitz: 4 mi. N. of Kelso, *Keck 5213;* Woodland. Oregon. Clatsop: Seaside. Tillamook: Garibaldi. Marion: Chemawa. Lincoln: Taft, *Keck 5217*. Douglas: mouth of Umpqua River, *T. Howell*. Coos: McKinleyville. Curry: Langlois; Gold Beach; mouth of Chetco River. California. Del Norte: S. of Klamath, *Keck 5225*. Humboldt: Scotia; Cape Mendocino; Shelter Cove. Mendocino: Westport; Fort Bragg. Sonoma: Duncan Mills.

Chromosome counts were made in meiotic divisions of plants from White Horse, Snohomish Co., Washington, and Trinidad and Van Duzen River near Carlotta, Humboldt Co., California, and in somatic plates in root-tips of plants from north of Fort Bragg and Jenner, California.

A collection from the Columbia plains, *Nuttall* (NY, Ph) is labeled and starred by Nuttall as his *A. heterophylla;* but Hall and Clements chose as the type of this entity the sheet in Gray Herbarium which has locality data corresponding to that in the original description, and this sheet is *A. Douglasiana* Bess. Nuttall lumped the two collections (and species) without detecting the importance of the differences between them.

Despite an exact duplication of habit, the more strongly discolored leaves, very narrowly cylindric and yellowish glabrate heads, and compact inflorescence of *Suksdorfii* serve to distinguish this species at a glance from *Douglasiana* in the field.

9. **Artemisia Douglasiana** Bess. in Hook., Fl. Bor. Amer. 1:323, 1833.

Figures 6, 10, and 17

Type statement: "North-West America. *Douglas, in Herb. Lindl.*"

Artemisia vulgaris var. *californica* BESS., Linnaea 15:91, 1841. Type locality: San Francisco.

A. heterophylla NUTT., Trans. Amer. Phil. Soc. II, 7:400, 1841, in part (as to the specimen at Gray Herbarium chosen by Hall and Clements as the type, not as to starred specimen at Philadelphia); not Bess., 1834.

A. ludoviciana var. *Douglasiana* D. C. EAT. in S. Wats., Bot. King's Expl. 183, 1871.

A. Kennedyi A. NELS., Proc. Biol. Soc. Wash. 18:175, 1905. The interior form of the species that has migrated eastward through the low northern Sierran passes. Type locality: Verdi, Washoe Co., Nevada.

A. vulgaris ssp. *heterophylla* HALL et CLEM., Carn. Inst. Wash. Publ. 326:76, 1923.

A. vulgaris var. *heterophylla* JEPS., Man. Fl. Pl. Calif. 1142, 1925.

A. vulgaris ssp. *Douglasiana* ST. JOHN, Fl. S. E. Wash. 422, 1937.

Stems 5–15(–30) dm. tall, stout but herbaceous to base, simple or sometimes ± branched, the branches erect to divergent; leaves all lanceolate to elliptic and entire, or oblanceolate to obovate in outline and coarsely few-lobed or toothed toward apex, with the margin extremely variable in outline, the entire lobes mostly lanceolate, 7–15 cm. long, 1–3(–5) cm. wide exclusive of salient lobes, those of the inflorescence gradually reduced in size, all strongly discolored, sparsely tomentulose to glabrous and green above, densely gray-tomentose beneath, usually plane; inflorescence a leafy open or dense elongated panicle, 3–15 cm. broad; heads medium-sized, erect or nodding; involucre campanulate, 3–4 mm. high, 2–3 mm. wide, ± tomentose, with 8–14 bracts; ray-florets 6–10; disk-florets 10–25. $n = 27$.

Washington to northern Baja California; rare east of the Cascadean-Sierran axis except about Lake Tahoe where it extends slightly into Nevada, and at elevations rarely up to 2000 m.; local in northern Idaho. Flowering from June to October.

"Rocky Mountains by streams," *Nuttall* (Gray, type of *A. heterophylla* Nutt. as fixed by Hall and Clements; tracing, C). Idaho. Kootenai: Lake Coeur d'Alene, 1892, *Aiton* (Po). Benewah: St. Joe River below St. Maries. Nevada. Washoe: Verdi, Sept. 29, 1904, *Kennedy 963* (RM, type of *A. Kennedyi*). Douglas: Glenbrook. Washington. Okanogan: Oroville, June 26, 1911, *Jones*. Yakima: Yakima region, *Cotton 876*. Klickitat: *Suksdorf 871*. Columbia River, North West America, 1830, *Douglas* (Herb. Benth., Kew, possibly of the type collection). Oregon. Hood River: Lookout Mt., 4000 ft., 1926, *Simon*. Multnomah: Portland, *Sheldon 11155*. Marion: Salem. Crook: Prineville, *Leiberg 837*. Klamath: Lake Ewana, *Lawrence 1196*. Douglas: Riddle. Coos: Marshfield, *House 4991*. Jackson: Trail Creek; S. of Ruch; Siskiyou Mts., *Heller 12635*. Curry: Brookings. California. Without exact locality, 1835, *Douglas* (Herb. Hook., Kew, possibly type collection of *A. vulgaris* var. *californica*). Modoc: Alturas, *Hall 11670*. Siskiyou: Yreka, *Butler 1798*. Lassen: Horse Lake. Shasta: Castella. Trinity: summit Scott Mts.; Yolo Bolly. Humboldt: Hoopa Valley; Van Duzen River opposite Buck Mt. Plumas: Red Clover Valley, *Heller and Kennedy 8876*. Tehama: Payne Creek. Butte: Jonesville, *Copeland in U. C. set 484*. Glenn: Chico Landing. Mendocino: Comptche, *Jones 29108*. Nevada: Donner Lake; Grass Valley. Yuba: Dobbins. Colusa: Princeton. Lake: Snow Mt.; Kelseyville. Eldorado: Fallen Leaf Lake; White Hall. Solano: Vallejo. Marin: Tiburon, *Heller 5724*. San Joaquin: Holt, plants over 11 ft. high, *Howell 5514*. Contra Costa: Berkeley. Mono: Walker River, 11 mi. S. of Coleville, *Wolf 3279*. Tuolumne: Confidence; Mather, *Keck 1336*. Mariposa: Yosemite Valley. Madera: 7 mi. from French Meadows, *Kennedy and Doten 420*. Inyo: Sobrina Lake, *Jones*. Fresno: Laton, 4 m. tall, *Hall*. Tulare: Hockett Meadows, 9400 ft., *Purpus 2095;* 10 mi. E. of Visalia. Kern: Rosedale; Tehachapi Pass. Santa Clara: Palo Alto, *Baker 1563;* Arroyo Bayo. Stanislaus: Adobe Creek, Red Mts. Monterey: Pacific Grove, *Heller 7195*. San Luis Obispo: Santa Margarita. Santa Barbara: Santa Maria; Santa Cruz Island, *Rand 71*. Ventura: Sespe Creek; Triunfo. Los Angeles: Mesmer, *Abrams 2955;* Claremont; Swartout Valley; Santa Catalina Island. San Bernardino: Victorville, *Parish 10583;* Mill Creek Canyon. Riverside: Keen Camp; Cold Water Canyon. Orange: Newport Beach. San Diego: Warner Springs. Baja California. Tia Juana; Rio Santo Domingo, *Wiggins and Demaree 4781;* Rancho San Jose, E. of San Telmo, *Wiggins and Demaree 4835*.

Chromosome counts were made on the following plants, all somatic counts on single plants from California stations unless otherwise indicated: Santa Barbara (also meiotic); Pismo Hills, 30 m. elev.; Halls Valley, Mt. Hamilton, 490 m. (two plants); Santa Cruz Mts. between Los Gatos and Glenwood, 450 m.; Mather, 1400 m. (two plants); Smith Peak, Yosemite National Park, 2200 m. (one plant somatic, one meiotic); Medford, Oregon, 415 m.

In the San Francisco Bay region, the leaves of *Douglasiana* are usually more lobed than elsewhere, but this deviation from the usual pattern is insufficient to warrant nomenclatorial recognition.

The hypothesis has been proposed by Clausen, Keck, and Hiesey (1940a, pp. 342–344), that *Douglasiana*, a hexaploid species of inland valleys and moderate altitudes on the Pacific slope, originated by amphidiploidy (addition of the chromosomes) from the coastal diploid species, *Suksdorfii*, and the interior montane tetraploid, *ludoviciana*, whose essential characters it recombines. Transplant experiments demonstrated that the tall *Suksdorfii* is unfitted to occupy higher elevations. It was even a poor survivor at the Mather transplant station at 1400 m. elevation where *Douglasiana* is native. The smaller statured *ludoviciana*, on the other hand, ranging widely toward the eastward,

has been able to occupy even alpine habitats. It enters the range of *Suksdorfii* in the Columbia River Gap, and here hybridization may have been possible. *Artemisia Douglasiana* is found in the geographically and climatically intermediate zone between the ranges of its presumed parents.

10. **Artemisia Prescottiana** Bess. in Hook., Fl. Bor. Amer. 1:324, 1833.
Figure 10

Type statement: "North-West America. *Douglas in Herb. Lindl.*" Known only from the type collection made in 1825 by David Douglas on the Quick Sand River, near the Grand Rapids of the Columbia. (This is near The Dalles, but whether from the Washington or Oregon side is undetermined.) The sheet in Bentham's herbarium at Kew has been studied. A note on it by R. A. Rolfe states that it exactly corresponds with the type of *A. Prescottiana* in the Lindley Herbarium. A drawing and fragment of this plant are at New York.

Stems 3–4 dm. tall, slender, several branching from the slender slightly suffrutescent base, striate, smooth and shining, like especially the under surface of the leaves very sparingly arachnoid-pilose, the very slender hairs mostly spreading; leaves 2–5 cm. long, less than 1 mm. wide, pinnatifid with 3–7 filiform caudate entire divaricate remote divisions 5–18 mm. long, or those of the inflorescence entire, green, the margin closely revolute; inflorescence racemose, sparingly leafy, the few erect heads on short filiform pedicels well spaced; involucre hemispheric, 3.5–4 mm. high, 4–5 mm. wide, green and shining, the 10 bracts very sparingly arachnoid-pilose, ± ciliate; ray-florets 6; disk-florets 23 (only one head counted).

I have seen no other specimen than the one in the Bentham herbarium that could be referred to this species, so it is assumed that it is a local endemic not as yet rediscovered, or that it is by this time extinct. The branching base is unique, slender branches developing from each of the lower nodes; the lowest and strongest become flowering stems, those a little higher are sterile almost capillary leafy shoots about 10 cm. long. The filiform and filiform-lobed leaves, which are not at all fascicled, and the pubescence are also unduplicated, and the racemose arrangement of the heads is only approached in forms of *A. Lindleyana* and *A. Michauxiana*, plants that otherwise have very little in common with this. In other words, while the floral characters plainly show that *A. Prescottiana* is a member of this complex, it does not seem to be very closely related to any other species.

11. **Artemisia Tilesii** Ledeb., Mem. Acad. St. Petersb. 5: 568, 1814.

11a. **Artemisia Tilesii** Ledeb. ssp. **typica** Keck nom. nov.
Figures 10 and 18

Type locality: Kamchatka. Type not seen.

Artemisia Tilesii LEDEB., *loc. cit.*

A. Tilesii var. *arctica* BESS. in Hook., Fl. Bor. Amer. 1:324, 1833. "Ex littoribus arcticis est var. ζ arctica—foliorum laciniis integerrimis magis distantibus obtusis brevibus, pericliniis floseulisque pallidis."

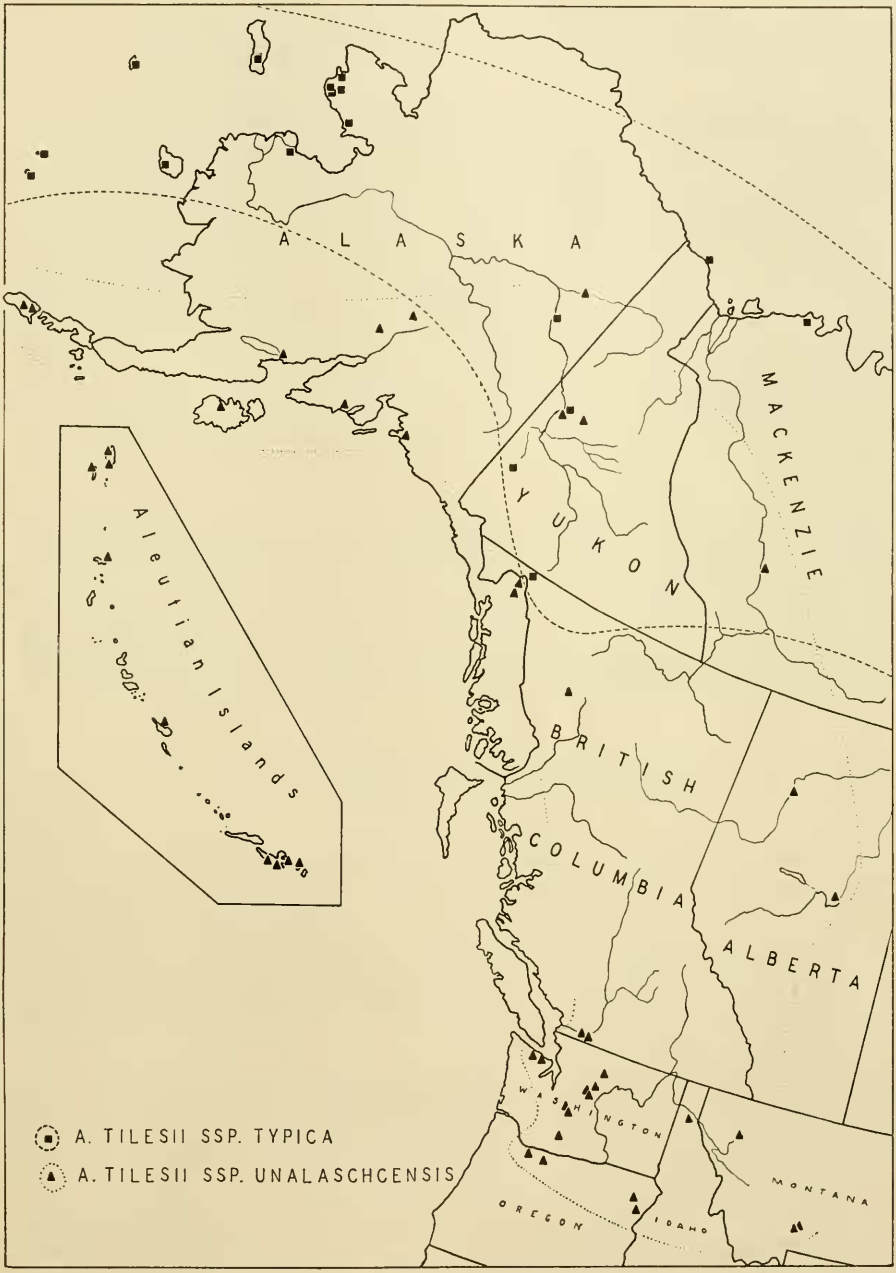


Figure 18. Distribution of *Artemisia Tilesii* in North America.

A. vulgaris var. *kamtschatica* BESS., Nouv. Mém. Soc. Nat. Mosc. 3:54, 1834.
A. vulgaris var. *Tilesii* LEDEB., Fl. Rossica 2:586, 1844–46.
A. vulgaris ssp. *Tilesii* HALL et CLEM., Carn. Inst. Wash. Publ. 326:72, 1923.

Stems 1.5–6 dm. tall, floccose when young but soon glabrate; leaves ovate to lanceolate in outline, deeply incised into 3–5 lanceolate attenuate sparingly toothed or dentately lobed divisions, the leaves of the inflorescence merely toothed or entire, all strongly discolored, green above, tomentose beneath; inflorescence a rather compact spike-like panicle often overtopped by the leaves; heads nodding, large; involucre hemispheric, 4–5 mm. high, 6–9 mm. wide, the bracts 12–28, ± anthocyanous, with broad scarious margin, glabrous and shining, or the outermost somewhat tomentose along midrib; ray-florets 9–25; disk-florets 20–100.

Nova Zembla, northern Siberia and Kamchatka to the Pribilof Islands, central and northern Alaska, Yukon Territory and east to Hudson Bay. Flowering from June to September.

North American stations: ALASKA. Bering Sea, *Macoun 89;* St. Lawrence Island; St. Matthew Island; Nunivak Island; Punuk Island; St. Paul Island; St. George Island; Kutzeblok; Taylor; Nome, *G. N. Jones 9211;* Norton Sound; Postoliak River, Yukon Delta; Circle. YUKON. Herschel Island, Arctic Ocean, Aug. 19, 1896, *A. Seale* (SU); Dawson, *Macoun 79012;* Lake Kluane to Don Jek River, 1920, *Müller.* BRITISH COLUMBIA. White Pass, *Eastwood 899.* MACKENZIE. Arctic shore between Mackenzie and Coppermine rivers, *Richardson* (NY); Coppermine River; Tree River; Hood River, Bathurst Inlet. MANITOBA. Churchill, Hudson Bay, lat. 58° 50′, *Macoun 79263.*

11b. **Artemisia Tilesii** ssp. **unalaschcensis** (Bess.) Hultén, Fl. Aleut. Ids. 327, 1937.

Figures 9, 10, and 17

Type locality: Island of Unalaska. Type not seen.

Artemisia Hookeriana BESS. in Hook., Fl. Bor. Amer. 1:322, 1833. The type, from Rocky Mountains, Canada, *Drummond* (Kew), has been studied. A sheet that matches the fragmentary type specimen so closely as to seem to be part of the same plant is labeled, R. Mts., Saskatchewan, 4–5 ft., *Drummond 23* (Kew). Leaves strongly discolored, bright green above, very white beneath, to 17 cm. long, many entire, linear-lanceolate, tapering to base and apex, some with 1–5 remote salient linear-oblong usually entire lobes 1.5–4.5 cm. long.

A. vulgaris var. *vulgatissima* BESS. in Hook., *ibid.* Not seen but probably referable here. Type statement: "North-West coast. *Douglas, in Herb. Lindl.*"

A. vulgaris var. *americana* BESS., Linnaea 15:105, 1841, in part, judging from the distribution and description. Not seen.

A. Tilesii var. *unalaschcensis* BESS., *ibid.* 106.

A. Tilesii var. *elatior* TORR. et GRAY, Fl. N. Amer. 2:422, 1843. "Subarctic America, *Richardson.*"

A. elatior RYDB., Mem. N. Y. Bot. Gard. 1:430, 1900.

A. unalaskensis RYDB., N. Amer. Fl. 34:266, 1916. Not based on *A. Tilesii* var. *unalaschcensis* Bess. 1841. Type collected on the island of Unalaska, Aug. 22, 1891, *Macoun 20625.* Leaves large, subpalmately parted or divided, the lobes again cleft.

A. Gormanii RYDB., *ibid.* 267. "Type collected in the Lake Iliamna Region, Alaska, September 1, 1902, *Gorman 281* (U.S. Nat. Herb. *no. 420345*)." Leaves more finely cut and

the divisions more slender and attenuate and the inflorescence less leafy than the type of *A. unalaskensis* Rydb. This is the form first described as *A. Tilesii* var. *elatior* Torr. et Gray.

A. obtusa Rydb., *ibid.* 274. This plant, known only from the type specimen, collected "on the Columbia" by Scouler, no. 234, is very doubtfully placed here. Scouler's collections were confined to the year 1825 and apparently were taken near the ocean along the coast from Nootka Sound, Vancouver Island, southward to the mouth of the Columbia, and at Fort Vancouver. The fact that this form has apparently not been recollected leaves its status in much doubt. The plant has leaves thicker in texture and more floccose on the upper surface, but otherwise cut about the same as those found in *A. Tilesii* ssp. *unalaschcensis.*

A. Tilesii var. *elatior* f. *pubescens* G. N. Jones, Univ. Wash. Publ. Biol. 5:254, 1936. A form from the Olympic Mountains in which the involucre is tomentose.

A. unalaskensis var. *aleutica* Hultén, Fl. Aleut. Ids. 327, 1937. Form with even the upper side of the leaves subtomentose-lanuginous. Type not given, but first plant cited was collected on Atka Island in 1834 by *Wrangell* (Leningrad). The variety is said to be limited to the middle and western Aleutians.

A. ludoviciana var. *americana* Fern., Rhodora 47:248, 1945. Both Fernald and the writer have tried to place Besser's variety on the basis of the original description alone, and the results do not agree. Fernald includes in it an assemblage of forms having leaves bright green above and panicles leafy and open, scattered from the Lower Athabasca River, northern Alberta, to northern Mexico. The writer assigns duplicates of the collections Fernald cites to five different units: the type, at least, to the present subspecies; most of the remainder to four subspecies of *A. ludoviciana*, namely, sspp. *mexicana* (Texas, New Mexico, Colorado, in part), *incompta* (Idaho), *typica* (Colorado, in part), and *sulcata* (Arizona). Fernald himself cites two of them again under his *A. ludoviciana* var. *mexicana.*

Stems 3–15 dm. tall, floccose when young but soon glabrate; leaves extremely variable, linear-lanceolate to oblanceolate, ovate, or subrotund in outline, the narrowest sometimes quite entire, the others bluntly or sharply few-toothed or -lobed to deeply pinnately, or commonly subpalmately, divided with some of the segments again toothed, lobed, or parted, those leaves with merely teeth or lobes often with wide lamina, those again lobed often with narrow lamina and segments, floral leaves entire or nearly so, all strongly discolored, green above (rarely tomentulose), tomentose beneath, plane, or the margin somewhat revolute; inflorescence a ± elongated narrow spike-like panicle, sometimes rather open, or a broad dense spike, well exceeding the leaves; heads erect or nodding, large; involucre hemispheric to broadly campanulate or turbinate, 3–5 mm. high, 4–8 mm. wide, the bracts 11–13, often darkly anthocyanous, sometimes green, with broad hyaline margin, glabrate or tomentulose; ray-florets 8–15; disk-florets 20–40. $n = 27$.

Northern Japan (Hokkaido, etc.) to Kamchatka, the Aleutian Islands, southern Alaska, Yukon and Mackenzie, southward to western Montana and northern Oregon; from sea-level in the north up to 1830 m. elevation in the south. Flowering from July to September.

North American stations: Attu Island (as *A. unalaskensis* Rydb.) and Attu, Agattu, Kiska, and Atka islands (as *A. unalaskensis* var. *aleutica* Hult.) all reported by Hultén, *loc. cit.* Unalaska Id.: Aug. 22, 1891, *Macoun 20625* (Canada, type of *A. unalaskensis;*

phototypes, C, CAS, NY, US), *Eyerdam 2346;* Dutch Harbor. Akutan Id., *Norberg 382.* Unimak Id.: False Pass, *Eyerdam 2250.* Kodiak Id.: Old Harbor. ALASKA. Porcupine River, *Turner;* Wonder Lake, McKinley National Park, *Mexia 2252;* Lake Iliamna region, sandy and rocky slopes above high tide south of Iliamna Point, Sept. 1, 1902, *M. W. Gorman 281* (US, type of *A. Gormanii;* phototypes, C, NY); Yentna District, above Morgan Creek; Seward; Cordova, *Mexia 2311;* Red River; Skagway; Chilkat Valley, *Walker 1077.* YUKON. Dawson, *Eastwood 455;* Klondyke. MACKENZIE. Fort Wrigley, *Preble and Cary 86.* ALBERTA. Peace River 10 mi. above Carcajou Settlement, *Raup and Abbe 4359;* Boiler Rapid, Athabasca River, *Preble and Cary 131.* BRITISH COLUMBIA. Cassiar District, pass near head Tset-ee-yeh River, a branch of Klappan River, *Preble and Mixter 640.* New Westminster: Chilliwack Valley, *Macoun 26350.* MONTANA. Flathead: McDonald Peak, Flathead Lake, *Jones 8775.* Gallatin: Bozeman, mountain canyons, 6,000 ft., *Blankinship 305.* IDAHO. Bonner: Lake Pend d'Oreille, *Sandberg et al. 754a.* WASHINGTON. Clallam: Sequim; Mt. Angeles, *Thompson 7502.* Chelan: Stehekiu; Mt. Stuart; Tumwater Canyon, *Thompson 8425.* Pierce: Mt. Ranier; White River. Yakima (?): Mt. Adams, *Gardner.* "Columbia" (River), *Scouler 234* (NY, type of *A. obtusa;* phototype and fragments, C). OREGON. Wallowa: Wallowa Mts., *Piper 2491.* Baker: Cornucopia, *Jones 29110.* Hood River: N. side Mt. Hood, *Thompson 3530.* Multnomah: Columbia River above Multnomah Falls, *Hall 11997.*

The chromosome number was determined at meiosis in a plant originating from seed of Hultén's plants from Unalaska grown at Stanford.

Both ssp. *typica* and ssp. *unalaschcensis* are highly variable, but they appear to represent fairly clear regional subdivisions of the species *Tilesii.* Some specimens, however, must be classified rather arbitrarily. The wide range of variation has prompted other workers to name many forms as the extended synonymy indicates. But this variation is extensive even in plants grown from single localities such as Unalaska Island, and there is no indication that there are any barriers to free interbreeding and recombination.

DISCUSSION AND CONCLUSIONS

In North America eleven species are recognized in the subsection *Vulgares* of *Artemisia*. All but one of these are polymorphic, several being highly so. Two contain recognizable geographic subspecies (there being seven such in *A. ludoviciana*). The conventional taxonomic treatment shows that additional cytogenetic investigations of this group are needed. In fact, the abundance of members of this complex in the North American flora, their great diversity of form, and their differences in chromosome number challenge our imagination and invite experimental studies.

An obvious opportunity for further work lies in a cytological survey of the subsection. Enough chromosome counts have been made to show that this is a typical example of the polyploid complex. There are special opportunities for evolution in such complexes, for a great diversity of habitats is occupied by forms closely enough related to allow some mixing of hereditary strains. This in turn produces variation and allows some of it to become fixed through genetical and ecological selection. It is to be expected that in such a complex both mutations of various sorts and hybridization have played major roles in building up the variation.

One of the ways in which sudden new steps in the evolutionary history may arise, and the variation increase, is through the crossing of two rather distantly related species. The probable origin of *A. Douglasiana* through the addition of all the chromosomes of two other species is an example. The strong circumstantial evidence for such an origin is given elsewhere (cf. p. 459), but here it should be pointed out that one of the supposed parents, *A. ludoviciana,* is exceedingly variable and occupies a wide range of habitats, while the other, *A. Suksdorfii,* is both morphologically stable and very limited in its choice of habitats. The evolutionary opportunities of *Suksdorfii* at the present time appear therefore limited, although this should not lead us to the conclusion that it is either a rare or decadent species. Also, if the theory of the origin of *Douglasiana* is correct, the chromosome set of *Suksdorfii* combined with that of *ludoviciana* to form the aggressive and variable species, *Douglasiana*. The evolution of a new species by the addition of the chromosomes of two others tends to revitalize the entire complex to which they belong. The potential significance of *Suksdorfii* in the evolutionary course of the complex is therefore enhanced through the chromosomes it probably contributed to *Douglasiana*.

The accompanying diagram, figure 19, attempts to show the North American members of subsection *Vulgares* placed very roughly in the relative positions they would assume on a map of the continent. The geographical ranges are much generalized, and accurate limits are to be found under the taxonomic treatment. Chromosome numbers are given where known. The arrows suggest possible courses of evolution as gathered from the available evidence on morphological and cytological relationships. The intangible impressions that come from an intimate study of a group have also played a part here.

In the case of *A. Douglasiana* mentioned above, arrows indicate its probable origin from *A. Suksdorfii* and *A. ludoviciana*. The subspecies of *ludoviciana* that seems to be the most likely forebear of *Douglasiana* is uncertain, but both sspp. *candicans* and *typica* are suggested. Aside from this case, in which

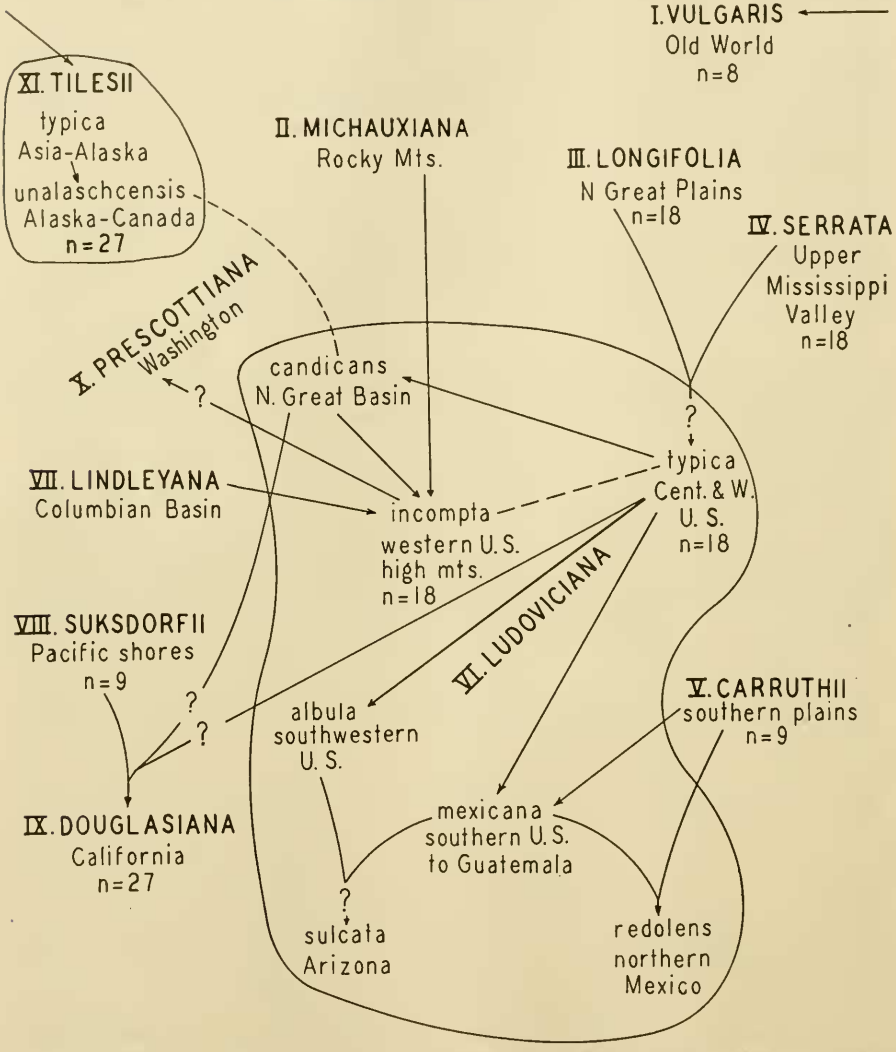


Figure 19. Chart of possible relationships, showing the relative geographical position and some chromosome numbers of the subsection *Vulgares* of *Artemisia*. See text.

the circumstantial evidence is strong, our present information is too fragmentary to indicate origins; therefore, for most of the systematic units more than one alternative must be considered.

In the other instances in the chart in which arrows from two forms point to a third one, amphidiploidy or even hybrid origin is not to be inferred,

although that possibility need not be ruled out. Such arrows merely indicate that on the present evidence it is difficult to determine the exact relationships and possible origins. Furthermore, it is to be readily granted that such variable units as *A. ludoviciana* sspp. *typica* and *mexicana* may have had polyphyletic origins.

The European source of *A. vulgaris* is indicated by an arrow, as is also the probable Asiatic origin of *A. Tilesii*. A broken line calls attention to the morphological-ecological similarity between *A. Tilesii* ssp. *unalaschcensis* and *A. ludoviciana* ssp. *candicans*. Possibly here is an evolutionary connection between *Tilesii* and the other American species.

Scarcely any two units in the North American assemblage are less alike than the only two known diploid species, *A. Suksdorfii* and *A. Carruthii*. Both of these occur on the periphery of the distribution of this complex and occupy extreme climates, the former, an equitable moist coastal zone, and the latter, dry semideserts. Accordingly, they show extreme differences in size, habit, and leaf characters, although they resemble each other in their few-flowered heads. These two species inhabit climates that must have been available from mid-Tertiary time, at least. It is of prime interest to find such ecologic specialization in species that have remained on the diploid level and likely are of great age. *Artemisia Suksdorfii* bears some morphological resemblance to *A. serrata*. The recurrence of this morphological type in the central states suggests that species or ecotypes of that type in the past may have occupied those parts of the North American continent where now the polyploid species are the only representatives.

The diversity of the North American diploids and the presence of another anomalous form like *A. Prescottiana* suggest that great gaps now exist in the evolutionary fabric of this group, making the present-day picture incomplete. Certainly the monophyletic origin of the subsection from any living American species appears quite impossible.

The North American diploids and the Eurasiatic diploid, *A. vulgaris* L., bear no close resemblance to one another. Other diploid progenitors of these must therefore have existed which now are lost.

The greatest diversity in the subsection *Vulgares* appears to be found in North America, and the known facts indicate that the American species (excepting *Tilesii*) originated in America. But, since the complex is distributed both on this continent and in Eurasia, the progenitors of the present-day diploids may have originated on either land mass and migrated across the Bering Straits. *Artemisia Tilesii*, which now is distributed across this migration bridge, appears to have closer ties in Asia than in America, and therefore may be considered as having originated in the west and moved eastward; but the Asiatic flora is not well known as yet, and *Tilesii* may prove to be of American origin. At all events, this highly polyploid species of aggressive distribution is not presumed to be the direct ancestor of any of the other American forms, but rather itself a derivative of the evolutionary stream.

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